

AN ABSTRACT OF THE THESIS OF

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Title: RESPONSES OF BUSH SNAP BEAN CULTIVARS (PHASEOLUS  
VULGARIS L.) TO PLANT POPULATION DENSITIES

Abstract approved: \_\_\_\_\_  
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The effects of plant population densities on the growth and development of six cultivars of bush snap beans (Phaseolus vulgaris L.) were studied in two field experiments. A systematic planting design was used to achieve a range of densities from 21- to 110 plants per m<sup>2</sup> and a rectangularity of approximately 1. Cultivars were selected for differences in their leaf sizes. For most of the important parameters analyzed, including pod yield, cultivar x density interactions were not statistically significant.

The pod yield-population density relationships were described by the equation  $w^{-\theta} = \alpha + \beta \rho$ , where  $w$  is pod yield per plants,  $\rho$  is population density and  $\theta$ ,  $\alpha$  and  $\beta$  are constants. The relationships were slightly parabolic with the cultivars having a common  $\theta$  of 0.854 in one experiment and 0.836 in the other. Variation in the  $\alpha$  and  $\beta$  values did not conform to the hypothesis that  $\alpha$  is a measure of genetic potential and  $\beta$  is a measure of environmental potential. The optimum population densities of the cultivars differed;

however, the same two cultivars produced the highest pod yields at all densities in both experiments.

Yield component analysis showed that the racemes per area increased toward an asymptote and the pods per raceme and average weight per pod declined linearly as density increased. Among cultivars, the component characteristic most closely associated with high pod yield, regardless of population density, was large pod size. Small leaved cultivars had greater numbers of racemes, but fewer pods per raceme and smaller pods.

Leaf area index (LAI) increased toward an asymptote as density increased. The relationship between crop growth rate (CGR) and the LAI was complex. It was interpreted in terms of source-sink interactions. The CGR was constant for LAI between 1.25 and 2.50 during the two-week period prior to bloom, but during the reproductive period, the CGR increased linearly as LAI increased to a maximum of 4.25. The constant prebloom CGR was attributed to the restricted branch development, i. e. low sink potential, of the higher densities that probably was caused by poor light distribution. The idea was presented that canopy light distribution may be influencing yield more by its effects on the initial development of a superstructure for reproductive growth than by its effect on the CGR during the reproductive period.

Population density did not influence the date of initial bloom, the number of nodes on the main stem or the basic pattern of dry

matter distribution.

When the cultivars were compared, high pod yield was found to be mainly a function of an early, concentrated development and growth of reproductive organs and a concurrent reduction in vegetative growth. The cultivars with higher leaf areas during the reproductive period had lower pod yields, because their high leaf areas had developed as a compensatory reaction to their poor initial reproductive development.

Cultivars did not differ in the rate of decline of their net assimilation rates (NAR) per unit increase in their LAI; however, at any given LAI the highest yielding cultivars had the highest NAR. Their high NAR were associated with low specific leaf areas (SLA). Small leaved cultivars had a slower rate of decline in branches per plant as density increased.

Responses of Bush Snap Bean Cultivars  
(Phaseolus vulgaris L.) to  
Plant Population Densities

by

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# RESPONSES OF BUSH SNAP BEAN CULTIVARS (PHASEOLUS VULGARIS L.) TO PLANT POPULATION DENSITIES

## INTRODUCTION

One important objective of crop production research is to increase the yield of marketable product from an area of land. The population density and the arrangement of plants are two factors that greatly influence yield.

Many experiments have been conducted to determine the optimum seeding rates for crops. During recent years, however, several technological developments have encouraged the consideration of higher plant densities and narrower row spacings than had been previously investigated. The improvement of crop environment, especially through the increased use of chemical fertilizers and irrigation, has enabled a unit area of land to support higher population densities. In addition, destructive mechanical harvesting has encouraged the use of higher plant populations as a means of increasing the amount of marketable yield available at a single harvest. The advent of effective chemical weed control has freed growers from the necessity of row-cropping to facilitate mechanical cultivation, and has allowed them to grow solid blocks of plants arranged equidistantly.

Plant population and arrangement research has been conducted in Oregon with several vegetable crops. The results of the studies

with snap beans, the most important vegetable crop of the state, have demonstrated the yield advantages of higher than normal plant populations arranged in an equidistant pattern or in narrow rows instead of the standard standard 36-inch rows.

Olericulturalists have encouraged vegetable growers to use a systems approach to vegetable production. This concept means that changes in one cultural practice should be integrated with changes in others in order to realize maximum yield benefits. Accordingly, a change in plant density and arrangement should be integrated with changes in other cultural practices, such as fertilization and irrigation.

A basic component of a crop production system is the cultivar. Many reports have indicated that the effect of plant population densities on crop yield was dependent on the crop cultivar. The responses of diverse snap bean cultivars to plant densities, however, have not been adequately investigated. Many of the previous studies with snap beans were conducted across a narrow range of populations and with rather similar cultivars. In addition, the data reported were usually limited to the marketable yields. Although this is an important parameter, especially to local growers, research that analyzes only crop yield does not provide much information to the scientists attempting to discover the basic causes for a yield response.



In plant density research, as well as other types of field research, yield should be analyzed as a function of the overall growth and development of the plants. The information derived from this type of analysis would give crop scientists insight into physiological aspects of crop yield and suggest experiments of a more basic nature. In addition, it would help them place the burgeoning volumes of information about isolated plant processes into the perspective of crop production.

Based on this philosophy of field research, a study was conducted to compare important growth and developmental responses of diverse snap bean cultivars to plant population densities, and to determine the relationships of these responses to marketable yield.

## REVIEW OF LITERATURE

### Plant Population Density and Crop Yield

#### General

Holliday (52) identified two basic types of relationships between plant population density and crop yield: the asymptotic in which yield rises to a maximum level and then remains constant at higher densities, and the parabolic in which yield rises to a peak and then declines at densities above an optimum. He said that the asymptotic relationship was characteristic of crops having a vegetative form of yield, and cited results from studies with potatoes, rape and kale to support this contention. He added that the parabolic relationship was typical of crops having a reproductive form of yield. The kernel yield of corn has shown this response (35, 42).

The relationship between bush snap bean yields and plant population density has been asymptotic in some studies (62, 81) and parabolic in others (73, 89). The results of the several studies are difficult to compare however, because of differences in the range of densities examined, in the method of harvest and in the maturity of the crop.

## Quantitative Models

Nelder (86) has criticized the use of tests of significant difference for interpreting the crop yield-population density relationship and has advocated the use of quantitative models.

Reciprocal equations, based on the relationship between the inverse of weight per plant and the plant population density, have been the most commonly used models because of their flexibility and possible biological significance (119). The first reciprocal model was derived independently by Shinozaki and Kira (97) in Japan, and by Holliday (52) in Great Britain. The basic form is:

$$w^{-1} = \alpha + \beta\rho \quad (A)$$

where  $\alpha$  and  $\beta$  are constants,  $w$  is the yield per plant and  $\rho$  is the population density (plants per unit area).

Although this model can describe an asymptotic relationship, it cannot describe the parabolic. To remedy this shortcoming, Holliday (53, 54) proposed an extension of the model to:

$$w^{-1} = \alpha + \beta\rho + \gamma\rho^2 \quad (B)$$

where  $\gamma$  represents a third constant. He said that this empirically derived reciprocal quadratic model was only an approximation to the true parabolic situation. Willey and Heath (119) demonstrated, however, that this equation could describe a wide range of yield-population

density data. Nelder (87) discussed the general usefulness of inverse polynomial models for describing a variety of quantitative relationships in crop research.

Bleasdale and Nelder (14) proposed a modification of equation A to:

$$w^{-\theta} = \alpha + \beta \rho^{\phi} \quad (C)$$

where  $\theta$  and  $\phi$  are additional constants. Experience demonstrated, however, that data were usually not sufficiently accurate to permit determination of specific values of both  $\theta$  and  $\phi$  (11, 15). In addition, Mead (78) showed that the ratio of  $\theta$  and  $\phi$ , rather than their absolute values, determines the fit of the model. Therefore, workers assumed  $\phi = 1$ , and simplified equation C to:

$$w^{-\theta} = \alpha + \beta \rho \quad (D)$$

where  $\theta \leq 1$ . Bleasdale (10) pointed out that when  $\theta = 1$ , the model describes the asymptotic yield-population density relationship, and when  $\theta < 1$  it describes the parabolic one.

Biological significance has been attached to the variation of the constants in the reciprocal models. Willey and Heath (119) reasoned that since:

$$Y = wp \quad (E)$$

where  $Y$  is the yield per unit area, then equation A could be expressed as:

$$Y = \frac{\rho}{\alpha + \beta \rho} \quad (F).$$

They pointed out that as  $\rho$  approaches 0,  $Y$  approaches  $\alpha^{-1}$ . Therefore,  $\alpha^{-1}$  has been interpreted as being indicative of the genetic potential of the plant. Willey and Heath acknowledged, however, that this interpretation failed to take into account the fact that yield per plant would level off at a  $\rho > 0$ .

Willey and Heath further demonstrated that as  $\rho$  increased,  $Y$  approached the asymptote,  $\beta^{-1}$ . The  $\beta^{-1}$  has been considered a measure of environmental potential because it defined the limit of yield obtainable on a unit area of land.

According to Mead (78), the interpretation of  $\alpha$  remains the same for equation D as for equation A. He said, however, that no simple practical interpretation of  $\beta$  can be made when  $\theta \neq 1$ . Nevertheless, it has still been viewed as a reflection of environmental potential (11, 89).

Bleasdale (11) was the first to present experimental evidence supporting the proposed biological significance of  $\alpha$  and  $\beta$ . Comparing three onion cultivars, he found they had a common  $\beta$  but different values of  $\alpha$ . He also found the  $\beta$  varied from year to year for any given cultivar. Nichols, (89) working with snap beans, and Hearn (48), working with cotton, found that soil fertility influenced  $\beta$  but did not effect  $\alpha$ . Bunting (22) used equation A to compare the effects of

plant population density on the shoot dry matter yields of three cultivars of maize. Although the cultivars differed greatly in the time of flowering, they had a common  $\beta$ . The later flowering cultivars had, however, lower values of  $\alpha$ . When results from different years were compared, the  $\beta$  was found to be higher in dry seasons.

Contrary to the previous results, Jones (62) found differences in both the  $\alpha$  and  $\beta$  when he compared two bush snap bean cultivars. Bleasdale and Thompson (15) reported similar results from a study with parsnips.

When equation D is used,  $\alpha$  and  $\beta$  values from different treatments cannot be compared unless  $\theta$  is invariant. Although common values of  $\theta$  were found in the reports previously discussed, some studies have shown systematic variation in this parameter. Fery and Janick (41) found that the  $\theta$  for the yield of marketable tomatoes declined for later dates of harvest. When the total fruit yield, green as well as ripe, was considered, the  $\theta$  stayed near 1 regardless of harvest date. They concluded the changes in the  $\theta$  for marketable fruit yield were related to yield concentration, earliness and the ability to maintain ripe fruit on the vine in a marketable condition. Hearn (48), working with cotton, found that  $\theta$  declined when the plants lost young fruit due to insect infestation, periods of drought, or mechanical removal. The  $\theta$  value was not influenced by soil fertility.

### Cultivar Interactions

Many plant population density studies have compared the yield responses of diverse cultivars. Fery and Janick (40) contrasted the responses of five tomato cultivars ranging in vine type from large indeterminate to dwarf. At low densities, the larger vine types had significantly higher yields than the dwarf or miniature. At higher densities, on the other hand, the yields of all cultivars approached a common asymptote. Similar results have been reported for parsnips (15) and bulb onions (11). Dwarf lines of maize had lower yields than normal lines at low population densities, but superior yields at high densities (88). Lang et al. (66) reported that the optimum population density, i. e. the density giving the maximum yield per area, was a function of cultivar in maize.

The crop yield-population density relationships of diverse cultivars of snap beans and other leguminous crops have been studied, however, the results have not been as definitive as those from tomato and maize. Johnson and Harris (60) compared the responses of four soybean cultivars having different dates of maturity. Although the interaction between cultivar and spacing was not statistically significant, the greatest yield differences among the cultivars were at the lowest density. The yield of an intermediate to late maturing cultivar reached the highest asymptote but it leveled off at the lowest density.

Matthews (74) compared the yield-population density responses of a normal and a luxuriantly vegetative snap bean cultivar. The pods were harvested three times from the luxuriant cultivar and five times from the other one. He reported that the yield of the luxuriant cultivar decreased proportionately more with increased spacing.

Mack and Hatch (73) planted several snap bean cultivars in equidistant spacings ranging from 4 x 4 to 9 x 9 inches. The yield at a single harvest was found to respond parabolically, with the optimum spacing between 5 x 5 and 6 x 6 inches. They found a significant difference between the yields of the cultivars at a narrow spacing but not at the wider spacings. They concluded that breeding lines should be evaluated under the selection pressure of high density conditions. A study by Jones (62) supported this conclusion. Working in Great Britain, he found that an inherently smaller snap bean cultivar had a lower yield than a normal line at low densities but approached a higher asymptotic yield at high densities.

### Yield Components

The components of yield are a group of plant organs having a direct mathematical relationship to yield (43). All factors that influence yield must operate through one or more of the components. Grafius has described methods of using the component configuration of yield as a tool for selecting breeding lines (43, 44).



The effect of plant population densities on the yield components of various legume crops has been discussed in several reports. Invariably, an increase in plant density reduced the number of pods per plant (29, 32, 62, 67, 73, 81). This reduction has been associated with a decline in the number of pod bearing branches per plant (50, 51, 62). Hodgson and Blackman (51) stated that the primary effect of increasing plant density on Vicia faba L. was a reduction in the number of nodes at the bottom of the plant to produce branches bearing mature pods. After observing several tomato cultivars having diverse growth habits, Fery and Janick (40), reported that the reduction in the number of branches per plant was least for the most compact lines. Lehman and Lambert (68) compared two soybean cultivars and found that the relative difference in the branch numbers decreased with increasing population density. Jones (62) theorized that the reduction in branching at higher densities would compress the flowering period of snap beans and result in a more uniform pod maturity.

Hodgson and Blackman (51) found that the number of flowers per plant of Vicia faba L. was reduced by increasing density. They attributed the reduction to a decreasing number of inflorescences rather than to a change in the number of flowers per inflorescence. Fery and Janick (40) observed no change in the number of flowers per inflorescence on tomato, but did report a decline in the number of flowers to set fruit with increasing density. On the other hand,

Mosley (81) reported that population density did not alter the percentage of flowers to set pods for snap beans.

The reports describing the effect of population density on the size of the reproductive organ have been inconsistent. The seed size of soybeans and dry beans declined with increasing density in some studies (29, 50) and remained constant in others (51, 67). The average pod size of snap bean has generally decreased at high population densities (4, 62, 73, 81). Mosley (81) attributed the decrease to a reduction in pod length. On the other hand, Atkin (5) and Cutcliffe (32) did not find any relationship between pod size of snap bean and population density.

Chung and Goulden (29) calculated standardized partial regression coefficients to compare the relative importance of the yield components of eight dry bean cultivars, growing at two densities. At the higher density, average seed weight was the component most highly correlated with the yields of the cultivars. At the lower density, the number of pods per plant was the most important component.

The variability found in the response of the yield components to plant density may be partly due to component competition and compensation. Negative correlations have been observed between components when plants were growing under competitive conditions but they have not been observed on widely spaced or unstressed plants (1). Adams (1) said that these responses indicate the correlations were

developmental rather than genetic, and attributed them to intraplant competition. He identified the competition "peck order" of bean (Phaseolus vulgaris L.) as (1) rapidly developing young pods, (2) un-open flowers, (3) open flowers, (4) young fertilized ovules in developing pods, (5) freshly pollinated embryos and very young pods.

Component compensation has been shown to occur when a component was developing below its potential level (1, 45). Adelana and Melbourn (2) removed 30% and 13% of the young ears of maize and got only a 19% and 3% yield reduction, respectively, because of a compensatory increase in grain size. Grafius (44) has stated that the universality of a cultivar was largely a function of the compensatory flexibility of its yield system.

Adams (1) and Grafius (43) have stated that understanding the sequential pattern of component development would aid the interpretation of the physiological basis for the component configuration of yield. Adams (1) said that the order of component development of dry beans is pod number, seeds per pod and then seed size. Bush snap beans (101) and runner beans (9) have been shown to flower and set pods in cyclic patterns. Only one peak of pod set occurred when mature seeds were allowed to develop in the original pods. Stobbe et al. (101) found that the cyclic pattern was compressed in time when temperature was increased.

Watada and Morris (111) reported that the growth pattern of a bean pod was sigmoid. The maximum pod length was attained approximately 13 days after bloom. After maximum length was reached, seed weight began to increase noticeably and the endocarp of the pod began to collapse. A great increase in  $\text{CO}_2$  evolution accompanied seed growth. The seed growth pattern was a double sigmoid.

### Physiological Aspects of Yield-Density Relationship

In reviews of the physiological aspects of crop yield, the yield has frequently been considered a function of three general processes: the interception of light energy, the fixation of this radiant energy into chemical bond energy by photosynthesis and the distribution and utilization of the fixed energy. In field research these processes have been described by growth analysis. The procedures used in this quantitative analysis of plant growth have been reviewed by Radford (94) and Watson (113).

### Leaf Area

The leaf area per unit area of land surface was termed by Watson (112) the leaf area index (LAI). Only one surface of the leaves has been used in calculation of LAI.

Studies of the relationship between LAI and crop growth rate (CGR) have shown the existence of an optimum level of LAI in some

cases and a critical LAI in others. In the optimum response, the CGR increased to a peak as LAI approached an optimum level and then declined when the LAI exceeded the optimum. Donald (33) theorized that the optimum LAI was attained when the lower leaves of a crop canopy were receiving only sufficient light to be just above the light compensation point. At higher LAI, he reasoned, the lower leaves would have a higher respiration rate than photosynthetic rate and this negative balance would reduce the total CGR. Watson and French (115) attempted to increase the total dry matter production of kale by repeated thinning of leaves to maintain a suspected optimum LAI. They achieved a 6% increase in production, including thinnings, during the first year of the study, but got no significant increase during the second year. Theoretical proof for the existence of an optimum LAI was provided by the primitive model of Kasanga and Monsi (63) relating crop production to light interception.

In the critical LAI response, the CGR increased toward a maximum as LAI approached a critical level and then remained constant as the LAI exceeded this level. A critical LAI has been described for clover (76), corn (121), cotton (71), soybeans (26, 96), peas (36) and snap beans (62). According to Broughman (17), the critical LAI was attained when 95% of the noontime incident radiation was being intercepted by the crop canopy. A critical LAI of approximately 4 has been reported for both snap beans (62) and soybeans (26, 96).

The validity of the optimum LAI concept has been questioned by several crop scientists. Brown and Blaser (19) and McCree and Troughton (76) have pointed out that the failure to include material that has abscised from the plant in the measure of total crop dry weight would result in an artificial optimum LAI. In addition, the failure to consider seasonal environmental changes, such as decreasing radiant flux, has been cited as a confounding factor (121). Two assumptions implicit in the theory of an optimum LAI were that the respiration rate of the leaves would be proportional to their dry weights and that all leaves would have a common light compensation point. McCree and Troughton (76) found, however, that the respiration rate of a leaf was correlated mainly to its gross photosynthetic rate and to only a small degree to its total dry weight. Another study has shown that the light compensation point is lower for leaves developing in a shady environment (71).

Loomis and Williams (70) de-emphasized the difference between the optimum and the critical LAI relationships, arguing that the important factor was finding the minimum LAI necessary to obtain the maximum CGR. They contended that this would be at 95% interception of light in both cases.

Many crop scientists have concluded that the major reason higher population densities and a more equidistant plant arrangement have increased yield was that these practices reduced the period

between planting and achievement of the critical LAI (55, 70, 81, 96, 110, 114). Weber et al. (117), working with soybeans, found that the plant populations and arrangements favoring a rapid attainment of a high LAI had the highest biological yields.

Noting that biological yield is a function of CGR and time, Watson (112) said that the LAI should be integrated over time in order to give a measure of a crops ability to intercept light throughout a season. He called the integration of LAI over time the leaf area duration (LAD). He reported that the mean yields of wheat, barley, potatoes and sugar beets were proportional to their mean LAD. Comparing several wheat cultivars, Welbank et al. (118) found that the biological yields were more closely related to their LAD than to their LAI. Musgrave (84) maintained that the yield benefits from improved irrigation and fertilization were often the result of increased LAD.

Almost all of the dry matter found in the grain of cereal crops has been found to be assimilated after flowering (72, 102). Thorne (102) said that the grain yields of wheat and barley are closely correlated with the leaf area after flowering but not the leaf area before flowering. Welbanks et al. (118) found that the grain yields of wheat cultivars were nearly proportional to their LAD after flowering. Adelana and Milbourne (2) reported, however, a substantial translocation of stored carbohydrate from the stem of maize to the grain.

In contrast to the previous results, some studies concluded that yield was not limited by either the LAI or the LAD. Uniformly distributed defoliation of up to a third of the leaves of soybeans and snap beans has not caused a significant reduction in yield (46, 75, 77). Wallace and Munger (106) could not find a high correlation between the leaf areas of five dry bean cultivars and their yields. Adelana and Milbourn (2) reported a wide variation in the ratios between the grain yields of six maize cultivars and their LAD after flowering. In fact, the cultivar having the highest yield had the lowest peak LAI and LAD.

Plant population experiments have also found LAI was not limiting marketable yield. Weber et al. (117) found that the maximum yield of soybean occurred at a population density having an LAI less than the maximum level. Mosley (81) calculated that variation in LAI accounted for less than 30% of the variation in snap bean yields associated with plant population density. Bleasdale (10) contended that leaf area would not limit the marketable yield of a crop except at densities too low to achieve a critical LAI. Shibles and Weber (96) found that over a wide range of population densities soybean plants were capable of producing an LAI above that required for 95% light interception. Bleasdale (10) suggested that a more productive area for research and development would be to analyze and improve the assimilatory efficiencies of crop canopies.



Johnston and Pendleton (61) analyzed the relative contributions of leaves located in different sections of the foliar canopy to soybean grain yields. They found that the leaf area subtending the central portion of the plant, and comprising 65% of the total, made the greatest contribution to yield. The upper leaves were most efficient, in terms of dry matter produced per leaf area, and the lower leaves were least efficient. The lower photosynthetic efficiencies of leaves existing nearer the bottom of crop canopies has been attributed to the effects of leaf age as well as the lower light intensities (3, 20, 92). Thrower (103) found that soybean leaves obtained the carbohydrates necessary for their early growth from the older leaves, and then began to export carbohydrates when they reached between  $1/3$  and  $1/2$  their final area. She said the leaves were exporting most actively soon after reaching their full size but afterwards the rate declined. Once the leaves were fully expanded they were no longer capable of importing carbohydrates.

### Leaf Area Ratio

The ratio between leaf area and total plant dry weight has been termed the leaf area ratio (LAR). A high LAR has been considered a desirable characteristic because it indicated the plant had a high photosynthetic potential in relation to its respiratory load. Wallace and Munger (106) found that the yields of dry bean cultivars were

more highly correlated with their LAR than with either their LAD or LAI. Buttery and Buzzell (27) reported, on the other hand, that selection for high yielding soybean cultivars had concomitantly reduced the LAR. In population density studies with pea, Eastin and Gritton (36) found that LAR was negatively correlated with CGR. This relationship may be explained by results from another study showing an inverse relationship between LAI and LAR (26).

#### Specific Leaf Area

The ratio of leaf area to leaf dry weight has been termed the specific leaf area (SLA). The inverse of SLA has been called the specific leaf weight (SLW).

The SLA has been shown to change during the course of crop development. Koller (65) found that the SLA of soybeans steadily declined until immediately prior to leaf senescence, and then it increased during leaf abscission. Eastin and Gritton (36) reported, on the other hand, that the SLA of peas increased sharply during the early development of the crop and afterwards remained relatively constant. Pearce et al. (92) reported that the SLA of alfalfa decreased with age on plants growing in a growth chamber but increased with age in unthinned field plots. They said that SLA was reduced by low light intensity resulting either from mutual shading of leaves or an artificial reduction in the intensity.

Differences have been noted in SLA among cultivars (27, 62). Buttery and Buzzell (27) compared parent soybean cultivars with their progeny and found that selection for improved yield had concomitantly reduced SLA. They suggested the use of this parameter as a selection criterion.

### Net Assimilation Rate

The discovery of the C-4 pathway of CO<sub>2</sub> fixation and the associated lack of photorespiration by certain plant species has increased interest in improving crop yields by increasing the photosynthetic efficiency of leaves (83). Marked differences in photosynthetic efficiency have been found among cultivars of soybeans and Phaseolus vulgaris L. (21, 27, 34, 62, 106).

The net assimilation rate (NAR) has been defined as the rate of increase of dry weight per unit of leaf area (113). This parameter has frequently been calculated in field research to estimate the photosynthetic efficiency of crop leaves. Donald (33) pointed out that the NAR value for a crop was an average value for all leaves. The NAR of Phaseolus vulgaris L., during early development, has been near 80 mg/dm<sup>2</sup>/day (81, 106).

The NAR of snap beans and similar leguminous crops has usually declined steadily during the course of crop development (25, 36, 56, 81, 113), however, Wallace and Munger (106) noted an increase during

the initial period of reproductive development for certain cultivars of dry bean. A precipitous decline in NAR has been associated with increasing population density early in the season, however, NAR was relatively constant later in the season (25, 36, 56).

The relationship between NAR and crop yield has been found to be neither simple nor direct. Buttery and Buzzell (27) noted a tendency to select for a higher NAR in soybean breeding programs, however, Evans and Dunstone (38) found that modern wheat cultivars had lower photosynthetic efficiencies than their wild progenitors. Curtis et al. (31), comparing 36 cultivars of soybeans, found that two cultivars assimilated  $\text{CO}_2$  at a rate approximately 25% greater than the others but produced lower yields of grain. These two cultivars had the lowest leaf areas.

Several studies have found a negative correlation between leaf area and NAR (36, 56, 81). The relationship has been attributed to the increased mutual shading at the higher leaf areas. The rate of decline in NAR per unit increase in LAI has been used as a measure of the canopy efficiency of crops (26, 116). Watson and Witts (116) reported the NAR of improved cultivars showed a slower rate of decline than the older standard ones. They attributed this to improvements of canopy architecture.

Watson (113) predicted that cultivars with a higher LAR would have a higher NAR, however, experimental results have shown the

opposite relationship (27, 36). The negative correlation between LAR and NAR has been ascribed to increased mutual shading at the higher LAR (108).

A report by Buttery and Buzzell (27) showed a significant negative correlation existed between the SLA and NAR of soybean cultivars. They found that SLA had a high heritability and suggested it would be a good characteristic for easy, indirect selection of photosynthetic efficiency. Dornhoff and Shibles (34) theorized that low SLA may be associated with a high cell surface to volume ratio, therefore, a lower mesophyll resistance to CO<sub>2</sub> diffusion.

### Leaf Angle

Several crop scientist have asserted that leaf angle was the foliar characteristic having the most immediate promise for increasing crop production (33, 69, 83, 108). Chandler (28) attributed the superiority of new high yielding rice cultivars mainly to their upright leaf habits.

Loomis and Williams (69) noted that the optimum leaf angle for a crop would vary according to such factors as species, solar angle and light intensity. According to several reports, the leaves of leguminous plants including Phaseolus vulgaris L., become light saturated at approximately 3000 ft-c. Beuerlein and Pendleton (6) found, however, that the leaves from the field-grown soybean plants

became light saturated at 10,000 ft-c and those of spaced plants were not light saturated at 15,000 ft-c. Computer models of crop canopies have shown that prostrate upper leaves would intercept an inefficiently high proportion of light, especially when the leaves are light saturated at rather low intensities (80, 121). Erect leaves would result in a near optimum light intensity over of greater leaf area. Pendleton et al. (93) planted two isolines of maize, one with normal and the other with erect leaves, at a moderate population density achieving an LAI of 4.1. The erectophile line gave a 41% higher grain yield, due mainly to a reduction in the number of barren plants. When they used mechanical methods to affect leaf angle, the normal plants yielded 10,700 kg/ha, plants with all leaves upright yielded 11,400 kg/ha and those with only leaves above the ear upright yielded 12,200 kg/ha of grain.

Other workers have suggested that leaf angle would not have an appreciable effect on crop growth except at high LAI. Montieth (80) calculated that the erectophile habit would not be beneficial until an LAI between 8 and 12 had been attained. Winter and Ohlrogge (122) achieved a range of LAI by varying the population density of a maize crop. Leaf angle was manipulated mechanically. They found that erect leaves decreased yield at LAI below 3 or 4 but increased it at LAI above 5. The optimum LAI for economic yield was always lower for the normal leaves. When the erect and normal canopies were

compared at their respective optimum LAI, the grain yields did not differ significantly. Montieth (80) stated that leaf angle was more significant in effecting instantaneous rates of photosynthesis than in influencing total yields at harvest.

### Leaf Size

Leaf size has been shown to influence light distribution in a crop canopy. Hicks et al. (49) found that light penetrated farther into the canopy of a narrow leaved soybean cultivar than it did into that of a normal line. The narrow leaved cultivar did not, however, produce a higher economic yield. Egli et al. (37) reported that on a leaf area basis, a narrow leaved soybean cultivar had a higher apparent rate of photosynthesis than a isogenic normal line, because it had superior light distribution in the crop canopy. They did not find a significant difference in the CGR of the two lines.

The leaf size of snap bean (81) and soybean (96) has been found to decrease as population density increased. In addition to having smaller leaflets, soybeans were found to produce longer petioles, giving the appearance of a less dense canopy. BATTERY (24) reported, however, that the leaf size of soybean was not influenced by population density.

### Plant Height

Increasing the vertical distribution of a crop canopy has been shown to increase light penetration (70). Several studies have found that plant height increased at higher population densities (49, 50, 60, 96, 117). According to Shibles and Weber (96), the tall plants made the foliar canopy of a soybean crop appear less dense. Hicks et al. (49) reported that tall determinate soybean cultivars developed greater LAI than short determinate types. Johnson and Harris (60) noted that the effect of population density on the plant height of soybeans was closely associated with its effect on economic yield. This was partly related to the effect of plant height on susceptibility to lodging.

### Distribution of Dry Matter

The manner in which a plant distributes dry matter may influence economic yield at least as much as the total dry matter it produces. Van Dobben (104) stated that the main contribution of plant breeders to improving cereal yields had been by increasing the proportion of the total plant dry weight represented by the grain. Shibles and Weber (96) examined the effects of plant population density and planting pattern on the grain yields of soybeans and concluded that the differences in seed yield were mainly due to differences in patterns



of dry matter distribution. The total dry matter production and the percentage of incident radiation intercepted was nearly the same for all treatments. Bleasdale (10), after a review of many population density experiments, asserted the parabolic response of reproductive forms of yield was due to the effects of density on the pattern of dry matter distribution. Nonetheless, Brouwer (18) was not optimistic about the potential for improving economic yields by altering patterns of distribution of dry matter. He reasoned that increasing distribution to the reproductive organs would necessarily reduce the flow of dry matter to the leaves, roots and other organs directly involved in total dry matter production.

Dry matter distribution involves the physiological process of translocation. Several basic investigations of translocation have been conducted on legumes. Using radiotracers, Biddulph and Cory (8) identified the translocated metabolites in Phaseolus vulgaris L. as predominantly sucrose plus a trace of two types of steroids. They were translocated mainly through the phloem traces.

Adams (1) said that a bean plant could be divided into several nutritional units, each unit being served by the same phloem traces. He identified the nutritional unit of bean as being a trifoliate leaf on the main axis together with a flower bearing raceme at its axil and a second smaller trifoliate borne on the peduncle subtending the basal floret. Bloomquist and Kust (16) reported a strong phyllotaxic pattern

of translocation in soybean plants. They found little radioactively labelled photosynthate on the side of the stem opposite the fed leaf. Johnston and Pendleton (61) found, however, that removal of leaves from one area of a soybean plant reduced seed yields in other areas as well as nearby.

The direction of translocation has been shown to be a function of the relative strengths and distances of the metabolic sinks (8). Soybeans have two distinct patterns of translocation, depending on the stage of plant development (16). Prior to bloom the metabolite went mainly to the meristematic regions above the leaf. After bloom it went primarily to the pods at the axil of the leaf and the second axil below the leaf. Seth and Wareing (95) presented evidence for hormonal control of translocation. They said that the directed transport of metabolites from leaves to pods was probably controlled by the high auxin content of the developing seeds in the pods. Johnson and Addicott (59) found that a high seed complement was required for cotton boll retention during periods of intraplant competition. Koller (64) reported that the seed growth rates of soybeans were primarily controlled by regulatory mechanisms within the seed.

Harvest Index (HI) has been defined as the ratio of the dry weight of the economic product to total plant dry weight. Wallace et al. (108) claimed that HI is a measure of a plants capacity to mobilize photosynthate and translocate it to the organs having economic

value. Some crop scientists have suggested that high HI be used as a selection criterion in breeding programs. Koller (64) reported that the HI of soybeans was constant over a wide range of environments and concluded it would have a high heritability.

High HI has not, however, insured a high crop yield. Wallace and Munger (107) compared the HI of eleven dry bean cultivars, growing at a single moderate population density, and found a poor correlation between harvest index and seed yield. In fact, the cultivar having the highest HI had the lowest yield. They stated that HI should be studied over a range of population densities in order to get a more realistic representation of the relationship of HI to economic yield. The reports of the effect of population density on HI have been contradictory. Neither Mosley (81) nor Jones (62) found a change in HI of snap beans over a wide range of densities. Nichols (89) reported, however, a slight decline in HI of snap beans at higher densities. Shibles and Weber (96) found that the HI of soybeans was reduced by either higher densities or narrower row spacings, but Leakey (67) observed no change for dry beans.

Shibles and Weber (96) attributed the reduction in HI of soybeans to an increase in competition between vegetative and reproductive growth at higher densities. They found that the period of vegetative growth was extended into the normal period of reproductive development at either the higher densities or higher rectangularities.

They suggested that cultivars that terminate vegetative growth when reproductive development begins would be adapted to high densities. Beuerlein et al. (7) tested this theory by manually removing all the branches developing on soybean plants after full bloom. This increased the yield at a high population density but reduced yield at a low density. Williams et al. (121) attributed the parabolic yield-population density response of maize to an excessive number of vegetative growing points at high densities competing with ear development. In accordance with this theory, compact lines of maize, which stop vegetative growth at the outset of ear development, have given higher yields at high densities than normal lines (88, 99). Contrary to the results with soybeans and maize, Wallace and Munger (107) were unable to find a significant relationship between the HI of eleven dry bean cultivars and indeterminate or determinate growth habit.

The relative lengths of the vegetative and reproductive growth periods can have a significant effect on HI. Evans and Dunstone (38) said that the higher HI of modern wheat cultivars was partly due to their longer periods of grain development. Koller (64) analyzed the growth of distinct strata of soybean plants. He found that the lower and middle stem sections partitioned 36% of their total dry weight into the grain, while the later developing branches and the upper stem section partitioned 47% into seed. He attributed the higher HI of the

later developing strata to a shorter vegetative growth phase relative to the reproductive phase. Other reports have suggested that early maturing cultivars tend to have higher HI (2, 107).

The number and potential size of the storage organs can have an important effect on HI and economic yield. Based on a thorough review of pertinent literature, Holliday (55) estimated that the potential grain yield of barley was 50% greater than the actual yields. He cited inadequate sink capacity in present cultivars. Nevertheless, the seeds of modern wheat cultivars were found to be as much as twenty times larger than those of their progenitors (38). Reduced sink capacity may be contributing to the parabolic yield-population density responses. Moss (82) reported that the reduction in the grain yields of corn above the optimum density was due to an increase in the number of barren plants.

The interaction between the utilization of dry matter by a sink and the production of dry matter by the leaves has been analyzed in several studies. Wareing et al. (109) found that partial defoliation of dwarf bean (Phaseolus vulgaris L.) plants caused an increase in the rate of photosynthesis of the remaining leaves. This response occurred even at saturating light intensities. Conversely, Moss (82) found that the rate of photosynthesis of tomato and maize leaves was reduced when the reproductive organs were removed. He attributed the reduction to an increase in the carbohydrate levels of the leaf

tissue. Sowell et al. (99) compared the stem fructose contents of a normal and a compact line of maize growing at high population densities. The frequently barren plants of the normal corn line had a higher percentage of fructose in the stem tissue than the ear bearing plants of the compact line. They concluded that the normal line could produce enough dry matter to fill an ear if the ovules had developed. Willey and Holliday (120) reported that a potential surplus of carbohydrates was available for grain filling of barley and that reduced grain yields at above optimum population densities was due to a limited storage capacity. Eastin and Gritton (36) observed an increase in the CGR and NAR of peas at the initiation of pod development. On the other hand, Nosberger and Thorne (90) found that floret removal from barley influenced dry matter distribution rather than NAR.

Some reports have suggested that inadequate sink capacity has not limited the HI and economic yields of legumes. Stobbe et al. (101) observed that many flowers and small pods abscised from snap bean plants. They attributed the drop of young reproductive organs to intraplant competition among the blossoms and a later abscission of small pods to the decline in photosynthetic potential of the plants. They contended that the maximum number of fruit was developing for a given plant size. This has been termed the capacity-set concept (30). Mosley (81) observed a nearly constant ratio of leaf area to pod weight for snap beans regardless of population density, suggesting

that sink potential was being limited at the higher densities.

The HI of a cultivar may be affected by the plants capacity to translocate metabolites. Evans et al. (39) observed that the phloem traces of modern wheat cultivars had a greater cross-sectional area per stem than those of their progenitors. Van Steveninck (105) found that the later flowers of lupine grew slower because of poorer vascular differentiation toward to apex of the raceme.

## MATERIALS AND METHODS

### General

Two field studies were conducted during the 1972 season at the Oregon State University Vegetable Research Farm at Corvallis. The plots were located on a Chehalis silt loam soil, which had been left fallow the previous summer after harvest of a crop of winter wheat. Fertilizer was broadcasted at a rate of 100 kg N, 132 kg P and 83 kg K per hectare and disced into the soil prior to planting. Weeds were effectively controlled by a pre-emergence spray of DNBP amine at a rate of 4 kg per hectare. Irrigation water was applied with overhead sprinklers at intervals of approximately 7 days or as needed. Delmhorst electrical resistance gypsum blocks were used to aid in scheduling irrigations. At least 2.5 cm of water was applied per irrigation.

Both studies were factorial experiments; the factors being cultivar, plant population density and sampling date. A split plot design was used, with cultivar and sampling date combinations as the main plots and population densities as the subplots. The main plots were replicated three times in randomized complete blocks.

Five cultivars were investigated in Experiment 1: 'OSU 1604,' 'OSU 58,' 'Gallatin 50,' 'L-1' and 'Keystone 4672.' In Experiment 2, 'L-81' was substituted for 'L-1.' 'Keystone 4672,' 'L-1' and 'L-81'



were selected for these studies because of their compact growth habits and small leaves. They were experimental lines, having no commercial use. 'L-1' and 'L-81' were developed at the New York Agricultural Experiment Station and 'Keystone 4672' was developed by the Keystone Seed Company. 'Gallatin 50,' 'OSU 1604' and 'OSU 58,' were selected to represent standard bush snap bean cultivars in terms of growth habit and leaf size. The two 'OSU' lines were developed at Oregon State University by W. A. Frazier. 'Gallatin 50,' a 'Tendercrop' type bean, was introduced in 1961 by the Gallatin Valley Seed Company and has been an important commercial cultivar in Oregon.

The systematic planting design type la of Nelder (85) was used in these studies in order to obtain a great number of population densities with a minimum number of guard plants. Because of the appearance of this design, it has been referred to as a fan. Each fan represented a main plot of the split plot design. The fans used in these experiments were composed of thirteen, internal, concentric arcs with the following plant spacings and densities:

Arc	Spacing (cm <sup>2</sup> per plant)	Population Density (plants per m <sup>2</sup> )
1	63.12	158.42
2	75.80	131.92
3	91.04	109.84
4	109.39	91.42
5	131.31	76.16
6	157.75	63.39
7	189.63	52.73
8	227.77	43.90
9	273.62	36.55
10	328.65	30.43
11	394.52	25.35
12	473.97	21.10
13	569.43	17.56

The plants were arranged in an approximately square pattern, i. e. rectangularity of 1. The fans used in Experiment 1 had 7 radials or spokes, and those used in Experiment 2 had 9.

An analysis was made of the dry weights of the individual plants of a fan to determine the number of guard plants required to eliminate border effects. Based on this analysis, only arcs 3 through 12 were sampled. In addition, two outside radials on both sides of the fans were left as guards.

The fans were planted by hand, using a marked wire system to locate planting positions (12). The beans were planted approximately 3 cm deep. Replications 1, 2 and 3 of Experiment 1 were planted on May 26, 27, and 28, respectively. The three replications of Experiment 2 were planted from June 19 through June 23.

Shortly after emergence, the plants were thinned to leave one healthy plant at each position. The positions at which no healthy seedlings had developed were marked with a small wooden stake. The eight plants surrounding this stake were not included in the samples.

### Collection of Data

Four sampling dates were included in the original designs of both experiments. Due to poor germination in Experiment 1, however, only the data from the final sample date, August 2, were statistically analyzed and reported herein. In Experiment 2, the sampling dates and the associated stages of plant development were:

Sample	Date	Days from Seeding	Stage of Development
1	July 19	28	Two weeks prior to bloom
2	August 2	42	Initial bloom
3	August 17	57	Midpoint of pod development period
4	August 30	70	Pods mature to slightly over-mature

Samples were taken by cutting the acceptable plants at their cotyledonary nodes. The plants of an arc were tied together to form a bundle representing a specific treatment-replication combination. The

bundles in Experiment 1 generally included three plants and those of Experiment 2, five plants.

Samples were taken prior to 1000 hrs of the designated days. Shortly after being procured, the samples were put into plastic bags, sealed and placed in cold storage at 7°C. At the later sampling dates, the plants were sometimes kept in cold storage for up to a week before the growth data were collected. This hiatus caused no apparent change in the plant material.

The plants of a sample were separated into their constituent parts and the number and sizes of various foliar, reproductive and structural organs were calculated. Foliar parameters included leaf number, leaf area and leaf dry weight. In order to be included in the foliar analysis, the leaflets of 'OSU 1604,' 'OSU 58' and 'Gallatin 50' had to have a basal width of over 2.5 cm, and those of 'L-81' and 'Keystone 4672' had to be over 1.9 cm. Leaflets that were senescent, to the extent that at least 1/3 of their total area was yellow or necrotic, were judged non-functional and were not included in foliar measurements. The leaf number was the total number of trifoliate leaves and monofoliate primary leaves. Leaf areas were measured with an air-flow planimeter (58). The leaf dry weights, as well as the dry weights of the other plant parts, were determined after drying the samples for at least 48 hrs at 80°C in a forced-air tunnel dryer.

Measurements of reproductive development were made in Experiment 1 and at samples 2, 3 and 4 of Experiment 2. Flowers displaying white petals were judged to be in bloom. Pods greater than sieve size 1 were counted in Experiment 1 and those greater than 2.5 cm in length were counted in Experiment 2. The sieve sizes of all pods were measured with a small hand grader. A raceme was defined as an inflorescence either terminating a stem or emanating from the axil of a leaf on a visible peduncle. All of the pods developing distal to the uppermost leaf on a stem were considered to be part of the same raceme unless they were developing on a distinctly separate peduncle. This criterion differed from that of Ojehomon (91), who considered the floral triad developing in the axil of an uppermost leaf as separate from the terminal raceme, although the peduncle was not visible. Only the racemes with acceptably sized pods were counted.

The stem and structural measurements included the stem length, number of nodes and number of branches. Stem length was measured from the cotyledonary node to the tip of the terminal raceme of the main stem. The number of nodes on the main stem prior to the formation of the terminal raceme was counted using the node from which the primary leaves had developed as number one. A branch was defined as an axillary shoot originating from the main stem and possessing or having possessed at least one acceptable leaf.

In addition to the dry weights of the acceptable leaves and pods, the dry weight of all remaining above-ground plant parts was measured. The bulk of these miscellaneous parts consisted of the stems, pedicels and peduncles, however, the unacceptable leaves and pods were also included.

Several growth analysis parameters were calculated from the raw data using the classical equations presented by Watson (113) and recently reviewed by Radford (94):

$$NAR = (w_2 - w_1)(\ln L_2 - \ln L_1) / (t_2 - t_1)(L_2 - L_1)$$

mean crop growth rate

$$CGR = (W_2 - W_1) / (t_2 - t_1)$$

mean relative growth rate

$$RGR = (\ln w_2 - \ln w_1) / (t_2 - t_1)$$

mean leaf area index

$$LAI = (LAI_2 - LAI_1) / (\ln LAI_2 - \ln LAI_1)$$

leaf area ratio

$$LAR = L/w$$

specific leaf area

$$SLA = L/Lw$$

harvest index

$$HI = w_{\text{pods}} / w_{\text{total}}$$

where  $w$  = total dry weight per plant,  $L$  = leaf area per plant,  $L_w$  = leaf weight per plant,  $LAI$  = leaf area index,  $W$  = total plant dry weight per unit area,  $t$  = time in days and the subscripts 1 and 2 refer to the relative times of the samples.

### Statistical Methods

Analysis of variance for a split plot design was performed on most of the data from experiments 1 and 2 (98, 100). The complete validity of tests of significant difference depends on a homogenous error structure; particularly, the variances cannot be proportional to the expected values. As expected (86) much of the data from these population density experiments indicated such a proportionality. Transformation to natural logarithms was expected to solve this problem and it did for most parameters.

NAR, CGR and RGR were calculated using the mean data from three replications. The variability of the data prevented a meaningful statistical analysis of these parameters.

The modified reciprocal equation

$$w^{-\theta} = \alpha + \beta \rho$$

was used to compare the pod yield-population density responses of the cultivars. A weighted least squares regression was used to fit an optimum response curve for each cultivar (78, 86). The curves were analyzed to determine whether differences among their  $\alpha$ ,  $\beta$  and  $\theta$

values were statistically insignificant. The formal system of analysis, an abridgement of one presented by Mead (78), was as follows:

- 1) Fit  $\alpha$  and  $\beta$  for each cultivar using the best individual estimate of  $\theta$ .
- 2) Fit  $\alpha$  and  $\beta$  for each cultivar using the best common estimate of  $\theta$ .
- 3) Test for insignificant differences among the  $\theta$  values.

If a common  $\theta$  value was statistically acceptable, further tests using the common  $\theta$  were valid:

- 4) Fit all data sets using a common  $\alpha$  and individual  $\beta$  values.
- 5) Fit all data sets using a common  $\beta$  and individual  $\alpha$  values.
- 6) Fit all data sets using both common  $\alpha$  and  $\beta$  values.
- 7) Test for insignificant differences among  $\alpha$  and  $\beta$  values.



## RESULTS AND DISCUSSION

### Pod Yields

#### General

The analyses of variance revealed significant differences in pod yields per plant among both cultivars and plant population densities (Table 1). The pod yields of 'OSU 1604' and 'OSU 58' were superior to those of the other cultivars at all densities, in both experiments (Tables 2 and 3). Pod yields per plant decreased as population density increased. The lack of statistically significant interactions between cultivar and population density indicates the rate of decrease was the same for all cultivars.

The percentage of pods sieve size 4 or greater was used as a measure of crop maturity. In both experiments, the crop was slightly past marketable maturity. The variability of sieve size distributions made interpretation of the yield responses difficult (Tables 2 and 3). For 'OSU 1604' and 'OSU 58,' the percentage of size 4 or greater pods decreased as density increased in Experiment 1, but the opposite trend was observed in Experiment 2. The sieve size distributions of 'Gallatin 50' and 'Keystone 4672' were not effected by population density in Experiment 1, but the percentage of size 4 or greater pods increased with increasing density in Experiment 2. An

inconsistent effect of population density on sieve size distribution has also been reported by Mack and Hatch (73). The inconsistency could result from cyclic patterns of pod set.

Table 1. Analysis of variance of pod yield per plant of snap bean.  
Experiments 1 and 2, 1972.

Source of Variation	D. F.	Mean Squares
<u>Experiment 1</u>		
Cultivar	4	2.9020*
Error(a)	8	0.4211
Population density	6	4.4412**
Cultivar x Population	24	0.1039
Error(b)	60	0.1181
<u>Experiment 2</u>		
Cultivar	4	1.8557**
Error(a)	8	0.0661
Population density	9	2.2696**
Cultivar x Population	36	0.0240
Error(b)	90	0.0245

\*  $p < .05$

\*\*  $p < .01$

Table 2. Effect of plant population densities on the pod yields per plant<sup>z</sup> and the pod sieve size distributions<sup>y</sup> of five cultivars of bush snap bean. Experiment 1, 1972.

Population density (plants/m <sup>2</sup> )	OSU 1604		OSU 58		Gallatin 50		L-1		Keystone 4672		Population means	
	$\ln(w_p)$	% <sup>y</sup> ≥ 4	$\ln(w_p)$	% ≥ 4	$\ln(w_p)$	% ≥ 4	$\ln(w_p)$	% ≥ 4	$\ln(w_p)$	% ≥ 4	$\ln(w_p)$	% ≥ 4
91.42	1.302	54	1.447	63	1.072	69	0.351	37	1.075	60	1.049	57
76.16	1.488	52	1.713	61	1.360	41	0.806	30	1.091	55	1.291	48
63.39	1.694	59	1.917	69	1.462	71	0.077	21	1.574	66	1.345	57
43.90	2.005	61	2.020	74	1.671	50	1.356	39	1.755	58	1.763	56
36.55	2.165	56	2.263	78	1.945	60	1.595	37	2.127	56	2.019	57
30.43	2.485	63	2.504	81	2.305	69	1.646	28	2.341	65	2.256	61
21.10	2.759	65	2.697	75	2.503	56	2.056	28	2.551	60	2.513	57
Cultivar means	1.986	58	2.080	71	1.760	59	1.128	31	1.788	60		
LSD Cultivar yield means, 5% = 0.462 1% = 0.672												
LSD Population yield means, 5% = 0.251 1% = 0.334												

<sup>z</sup> Yield reported as the natural logarithm of pod dry weight (grams) per plant,  $\ln(w_p)$ .

<sup>y</sup> Sieve size distribution reported as the percentage of pods (%) sieve size 4 or larger.

Table 3. Effect of plant population densities on the pod yields per plant<sup>z</sup> and the pod sieve size distributions<sup>y</sup> of five cultivars of bush snap bean. Experiment 2, 1972.

Population density (plants/m <sup>2</sup> )	OSU 1604		OSU 58		Gallatin 50		L-81		Keystone 4672		Population means	
	ln(w <sub>p</sub> )	% <sup>y</sup> ≥ 4	ln(w <sub>p</sub> )	% ≥ 4	ln(w <sub>p</sub> )	% ≥ 4	ln(w <sub>p</sub> )	% ≥ 4	ln(w <sub>p</sub> )	% ≥ 4	ln(w <sub>p</sub> )	% ≥ 4
109.84	1.426	73	1.299	78	0.914	73	1.213	84	1.063	74	1.183	76
91.42	1.629	82	1.630	70	1.124	62	1.389	74	1.213	63	1.397	70
76.16	1.993	85	1.674	72	1.209	72	1.370	77	1.485	71	1.546	75
63.39	1.883	75	1.800	70	1.342	64	1.561	74	1.357	66	1.589	70
52.73	2.105	68	2.066	85	1.624	70	1.713	82	1.448	65	1.791	74
43.90	2.190	78	2.122	72	1.655	69	1.930	83	1.772	67	1.932	74
36.55	2.421	83	2.207	77	1.940	68	1.987	76	1.846	65	2.080	74
30.43	2.511	78	2.393	76	2.049	60	1.938	59	1.871	59	2.152	67
25.35	2.610	70	2.569	76	1.970	59	2.217	69	2.023	68	2.278	68
21.10	2.715	68	2.535	67	2.227	57	2.094	47	2.020	60	2.318	60
Cultivar means	2.148	76	2.029	74	1.605	65	1.741	73	1.610	66		
LSD Cultivar yield means, 5% = 0.153 1% = 0.223												
LSD Population yield means, 5% = 0.113 1% = 0.150												

<sup>z</sup>Yield reported as the natural logarithm of pod dry weight (grams) per plant, ln(w<sub>p</sub>).

<sup>y</sup>Sieve size distribution reported as the percentage of pods (%) sieve size 4 or larger.

### Quantitative Models

The pod yield-population density responses of the cultivars were further described and compared by fitting the data to the modified reciprocal equation:

$$w^{-\theta} = \alpha + \beta \rho$$

where  $w$  is the mean pod weight per plant,  $\rho$  is the population density and  $\theta$ ,  $\alpha$  and  $\beta$  are constant parameters for a given set of data. Although the analyses of variance did not reveal significant cultivar  $\times$  population density interactions, significant differences were found in the yield-population density responses of the cultivars when the data were fitted to this model.

Evidence of invariance among the  $\theta$ ,  $\alpha$  and  $\beta$  parameters of the different cultivars was sought. Fittings of the best individual values of  $\theta$  were compared to the fittings with a common  $\theta$ : the arithmetic mean of the individual values of  $\theta$  (Table 4). The fittings with a common  $\theta$  value of 0.854 in Experiment 1 and 0.836 in Experiment 2 did not differ significantly from the fittings with the individual  $\theta$ . Experience showed, however, that a wide range of common  $\theta$  values, including  $\theta = 1.0$ , gave acceptable fittings. Several workers have noted imprecision in the determination of  $\theta$  by an iterative technique (42, 48, 89).

Table 4. Comparison of fits with best individual and with common  $\theta$  values (individual  $\alpha$  and  $\beta$  values for each variety). Experiments 1 and 2, 1972.

Variety	<u>Experiment 1</u>		<u>Fit with common <math>\theta</math></u>	
	<u>Best Fit</u>			
	$\theta$	$RSS/\theta^2$	$\theta$	$RSS/\theta^2$
OSU 1604	1.02	0.0102	0.854	0.0125
OSU 58	1.01	0.0125	"	0.0133
Gallatin 50	0.84	0.0635	"	0.0635
L-1	0.76	0.1268	"	0.1280
Keystone 4672	0.64	0.0551	"	0.0600
Totals and (degrees of freedom)		0.2681 (20)	--	0.2773 (24)

Variety	<u>Experiment 2</u>		<u>Fit with common <math>\theta</math></u>	
	<u>Best Fit</u>			
	$\theta$	$RSS/\theta^2$	$\theta$	$RSS/\theta^2$
OSU 1604	0.69	0.0521	0.836	0.0528
OSU 58	0.76	0.0347	"	0.0349
Gallatin 50	0.84	0.0433	"	0.0433
L-81	0.86	0.0547	"	0.0547
Keystone 4672	1.03	0.0627	"	0.0634
Totals and (degrees of freedom)		0.2475 (35)	--	0.2491 (39)

<sup>z</sup>RSS = residual sum of squares

A  $\theta < 1$  indicates the pod yield-population density relationship was parabolic. Mack and Hatch (73) have also reported a parabolic response for snap beans in Oregon. Nichols (89), using the allometric relationship between pod weight and total plant weight (13), calculated a  $\theta = 0.896$  for snap beans. On the other hand, Mosley (81) and Jones (62) have reported an asymptotic pod yield-population density relationship. Jones calculated  $\theta = 1$ . He said, however, that treatment variability may have prevented the accurate determination of  $\theta$  and added that " $\theta < 1$  could be appropriate.

Using the common  $\theta$ , the  $\alpha$  and  $\beta$  of the cultivars were calculated and tested for invariance (Table 5). In Experiment 1,  $\alpha = 0.0283$  was acceptable for all cultivars, but in Experiment 2 the  $\alpha$  differed significantly (Table 6). Significant differences were found among the  $\beta$  in both experiments. The two OSU lines had the lowest  $\beta$  in both experiments and the lowest  $\alpha$  in Experiment 2.

Although the common  $\alpha$  in Experiment 1 implies all five cultivars had a common genetic potential, this result probably has no practical significance. The  $\alpha$  is a measure of extrapolated yield per plant at  $\rho = 0$ . It does not take into account the fact that yield per plant would become constant at  $\rho > 0$ , because of a lack of interplant competition (119). The density required for the onset of interplant competition could be a function of cultivar.

Table 5. Comparison of fits for various  $\alpha$  and  $\beta$  combinations, assuming a common  $\theta$  value. Experiments 1 and 2, 1972.

A Experiment 1 ( $\theta = 0.854$ )

Form of Fit	D.F.	RSS <sup>x</sup>	RMS <sup>y</sup>	F <sup>z</sup>
(1) $\alpha$ and $\beta$ invariant	33	2.4659		
(2) $\alpha$ invariant	29	0.3152		
(3) $\beta$ invariant	29	0.8703		
(4) Individual $\alpha$ and $\beta$	24	0.2773	0.01155	

Sources of Variation

Variation of $\alpha$ , (2)-(4)	4	0.379	0.00948	0.8208 ns
Variation of $\beta$ , (3)-(4)	4	0.5930	0.14825	12.8355*
Variation of $\beta$ assuming $\alpha$ invariant, (1)-(2)	4	2.1507	0.5378	46.5628**

B Experiment 2 ( $\theta = 0.836$ )

(1) $\alpha$ and $\beta$ invariant	48	2.7961		
(2) $\alpha$ invariant	44	0.5165		
(3) $\beta$ invariant	44	0.4248		
(4) Individual $\alpha$ and $\beta$	39	0.2491	0.00639	
Variation of $\alpha$ , (2)-(4)	4	0.2674	0.06685	10.4617*
Variation of $\beta$ , (3)-(4)	4	0.1757	0.04393	6.8748*

<sup>x</sup> RSS = residual sum of square

<sup>y</sup> RMS = residual mean square

<sup>z</sup> F-ratios are calculated as the ratios of difference mean squares to error mean square about curves fitted with individual  $\alpha$  and  $\beta$  values (line 4).



The variations in  $\alpha$  and  $\beta$  do not support the contention that  $\alpha$  is a measure of genetic potential and  $\beta$  is a measure of environmental potential (11, 22, 119). The results do agree, however, with the observations of Jones (62), who compared two snap bean cultivars and found differences in both their  $\alpha$  and  $\beta$ .

The optimum plant population density, i. e. the density giving the greatest pod yields per area, was calculated with the constants from the modified reciprocal equation by

$$\rho_{\text{opt}} = (\alpha\theta)/\beta(1-\theta)$$

The pod yield per plant at the optimum density was calculated by

$$w_{\text{max}} = (1-\theta/\alpha)^{1/\theta}.$$

In Experiment 1, the optimum population densities of the cultivars were a function of their  $\beta$  values. The optimum densities of OSU 1604 and OSU 58 were approximately 52 and 57 plants per m<sup>2</sup>, respectively, and those of 'Gallatin 50' and 'Keystone 4672' were 41 and 43 plants per m<sup>2</sup> (Table 6). Mack and Hatch (73) reported the average optimum population density for seven snap bean cultivars was approximately 65 plants per m<sup>2</sup>. Because the  $\alpha$  was constant in Experiment 1, the pod yield per plant at the optimum densities was 6.83 grams for all cultivars. When the yields per area of the cultivars were compared at their respective optimum densities, the maximum yields of the 'OSU' lines were superior. Figure 1 illustrates the pod yield-population density responses of the cultivars, based on the  $\alpha$ ,  $\beta$  and  $\theta$

Table 6. The fitted values of  $\alpha$  and  $\beta$  together with the calculated optimum densities and maximum yields.

Cultivar	$\theta$	$\alpha$ ( $\times 10^{-2}$ )	$\beta$ ( $\times 10^{-3}$ )	$P_{\max}$ (Plants/m <sup>2</sup> )	$w_{\max}$ (g/plant)	$Y_{\max}$ (g/m <sup>2</sup> )
Experiment 1						
OSU 1604	0.854	2.831	3.204	51.67	6.83	352.9
OSU 58	"	"	2.914	56.81	"	388.0
Gallatin 50	"	"	4.075	40.63	"	277.5
L-1	"	"	6.534	25.34	"	173.1
Keystone 4672	"	"	3.890	42.56	"	290.7
Experiment 2						
OSU 1604	0.836	5.996	2.076	147.26	3.33	490.7
OSU 58	"	6.612	2.304	151.04	2.96	447.7
Gallatin 50	"	8.409	3.495	122.66	2.22	272.7
L-81	"	11.112	2.348	241.29	1.59	384.4
Keystone 4672	"	12.668	2.560	260.42	1.36	354.7

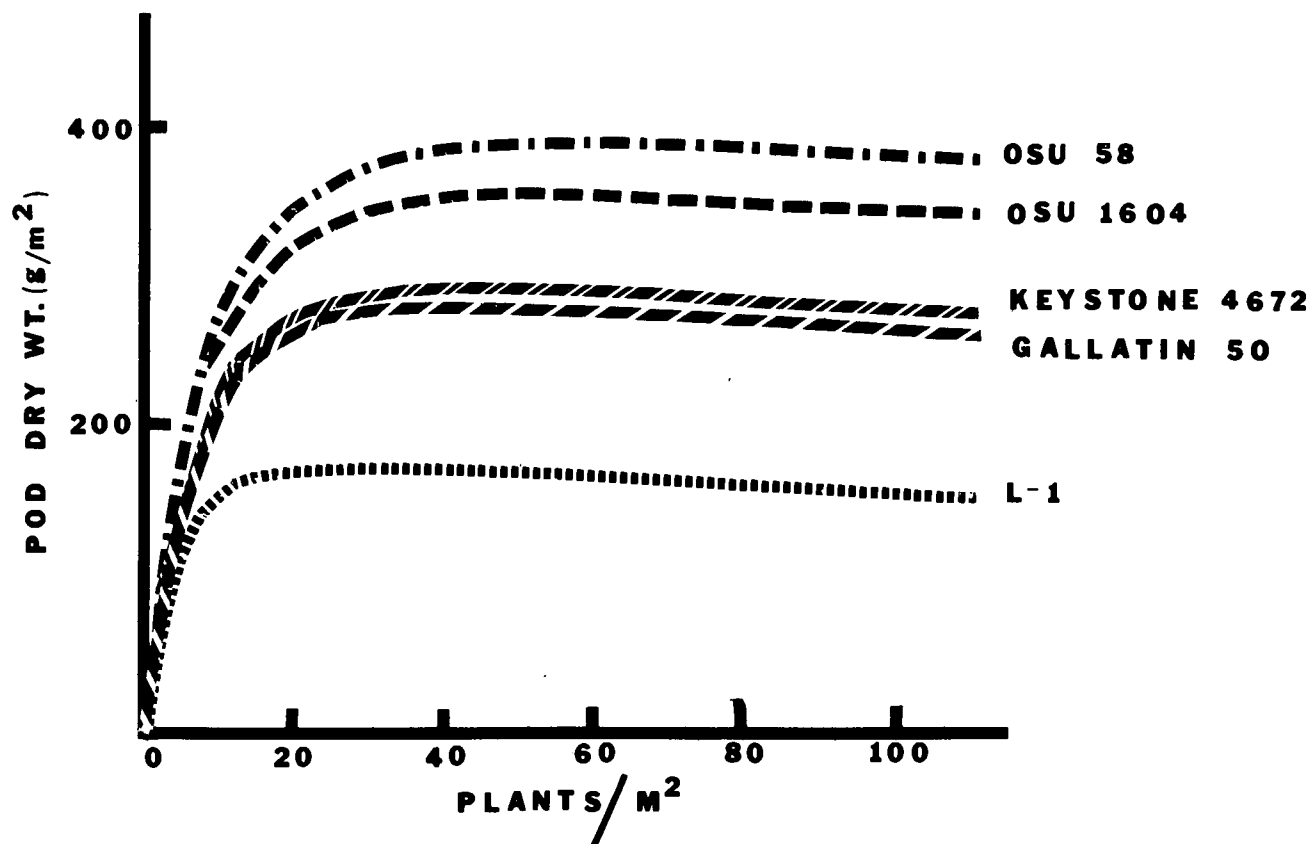


Figure 1. Effect of population density on the pod yields of five bush snap bean cultivars, as predicted by the data in Table 6. Experiment 1, 1972.

parameters in Table 6.

In Experiment 2, the optimum population densities of all cultivars were beyond the range of densities investigated (Table 6). The small leaved cultivars, 'Keystone 4672' and 'L-81,' had the highest optimum population densities, but the lowest pod yields per plant at their optimum densities. When all cultivars were compared at their optimum densities, the 'OSU' lines gave the highest maximum yields per area. Figure 2 illustrates the yield-population density responses of the cultivars in Experiment 2. Although the yields per area of the 'OSU' cultivars were superior to those of the other cultivars at all densities investigated, the differences between the 'OSU' cultivars and the small leaved cultivars were proportionately less at higher densities. At low densities, the yield per area of 'Gallatin 50' was greater than that of either 'L-81' or 'Keystone 4672.' At high densities, the latter two cultivars had superior yields.

The results of Experiment 2 generally agree with results from previous investigations. Fery and Janick (40) compared the yield-population density responses of several tomato cultivars, ranging in vine type from indeterminate to dwarf. They found that the differences between the yields per area of the cultivars diminished as density increased. Jones (62) compared two snap bean cultivars and found that the more compact one had a lower yield at the low densities but a higher yield at the high densities. A similar relationship has been

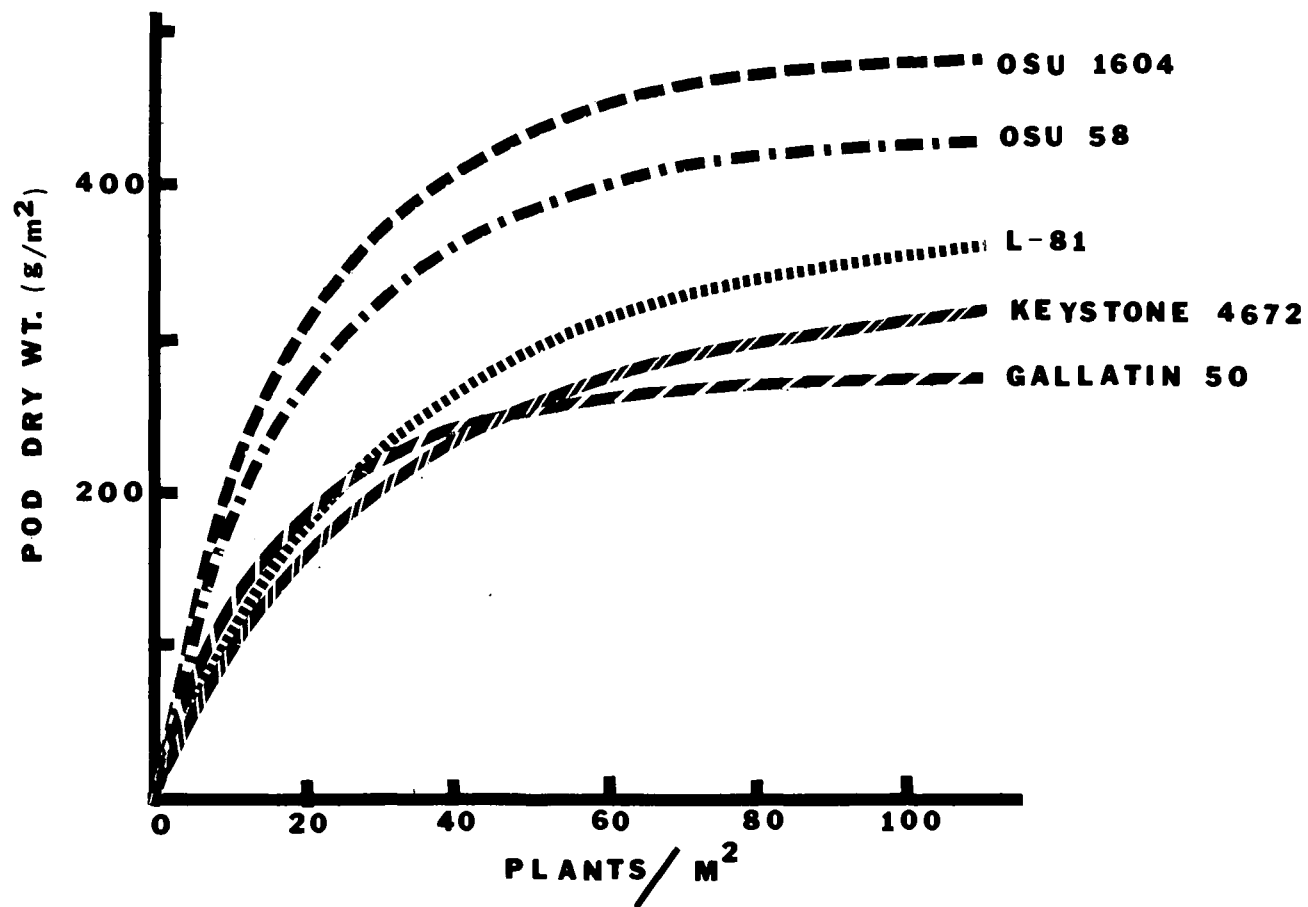


Figure 2. Effect of population density on the pod yields of five bush snap bean cultivars, as predicted by the data in Table 6. Experiment 2, 1972.

observed between dwarf and normal lines of maize (88). The results of Experiment 1, agree with the observations of Mack and Hatch (73). At a high density, they found a significant difference in the pod yields of two snap bean cultivars, but at a low density no difference was recorded.

### Reproductive Development

In both experiments, 'OSU 1604' and 'OSU 58' started to bloom approximately 3 to 4 days before 'Gallatin 50' or 'Keystone 4672' (Table 7). On the basis of daily observations, plant population density did not effect the initial date of bloom.

Table 7. The number of days from planting until the initial bloom of five bush snap bean cultivars. Experiments 1 and 2, 1972.

Cultivar	Experiment	
	1	2
OSU 1604	44	38
OSU 58	41	38
Gallatin 50	44	42
L-81	--	38
L 1	44	--
Keystone 4672	44	40

The cultivars differed significantly in their patterns of reproductive development after initial bloom. The development of reproductive sink potential was slower for 'Gallatin 50' and 'Keystone 4672' than for 'OSU 1604,' 'OSU 58' or 'L-81' (Table 8). Although 'Keystone

Table 8. The effects of cultivar and sample date (57 and 70 days from planting) on the pods per plant, pods per raceme and racemes per plant of bush snap beans. Experiment 2, 1972.

Cultivar	Pods/Plant		Pods/Raceme		Racemes/Plant	
	sample		sample		sample	
	3 (57 days)	4 (70 days)	3 (57 days)	4 (70 days)	3 (57 days)	4 (70 days)
OSU 1604	14.9	12.2	2.27	1.88	6.62	6.53
OSU 58	11.8	11.3	2.07	1.87	5.78	6.06
Gallatin 50	3.7	10.3	1.67	2.06	2.28	5.08
L-81	11.2	13.1	1.65	1.66	6.86	8.01
Keystone 4672	4.7	11.1	1.52	1.48	3.19	7.55

4672' and 'Gallatin 50' bloomed 40 and 42 days after planting, respectively, most of their raceme development and pod set occurred between samples 3 and 4; 57 to 70 days after planting. On the other hand, most of the reproductive sink potential of the 'OSU' cultivars developed prior to sample 3. L-81 also had a rapid development of reproductive sink, but it continued to develop racemes and set pods after sample 3. No data were taken in this study to determine whether the poor initial reproductive development of 'Gallatin 50' and 'Keystone 4672' resulted from the development of few flowers or from a poor set of pods.

The pods per raceme declined appreciably a short time before sample 4 (Table 8). In the final sample, many shriveled, seedless pods, over 4 cm in length, were observed. They were not included in the pod counts. Many of them had probably abscised before sample 4. Stobbe et al. (101) found that parthenocarpic bean pods often developed after high temperatures. They reported that the immature parthenocarpic fruit could remain attached to the plants for several weeks before abscissing. Iwami (57) attributed a late season abscission of reproductive structures to the decline in the plant productive capacity.



## Yield Component Configuration

### General

The effects of population density and cultivar on the component configurations of pod yield were difficult to interpret because of the cyclic patterns of pod set and the dynamic nature of the marketable product - an immature reproductive organ. The results of Experiments 1 and 2 are not directly comparable. In Experiment 1, only those pods greater than sieve size 1 were included in the component analysis. In Experiment 2, all pods greater than 2.5 cm length were included. Because of the standards used in Experiment 2, a large number of young pods, having little significance to marketable yield, were included in the sample. These small pods obscured the effects of cultivar and population density on the number of marketable pods per raceme and on the average pod weight. To solve this problem, analysis of covariance was used to adjust component means to a common sieve size distribution. The effort was only partially successful. In addition to the different standards used, the plants of Experiment 1 were harvested at a slightly earlier state of maturity. Notwithstanding these differences, the results from the two experiments showed the same basic response patterns.

## Racemes

Highly significant differences were found among both cultivars and population densities in the numbers of racemes per plant. The interactions of the two factors were not statistically significant at the 5% level of probability. The covariance adjustment of the means to a common sieve size distribution did not significantly change the results of Experiment 2.

Among cultivars, the number of racemes per plant was inversely related to leaf size. The two small leaved cultivars, 'L-81' and 'Keystone 4672,' had a significantly greater number of racemes in Experiment 2 and the same trend was apparent in Experiment 1 (Tables 9 and 10). The greater raceme numbers of the small leaved cultivars could indicate fuller light penetration into their foliar canopies (51).

In both experiments, the number of pod bearing racemes per plant declined exponentially as population density increased. When the natural logarithm of racemes per plant was regressed against the natural logarithm of population density, a significant linear relationship was found (Table 11). This indicates the racemes per area increased asymptotically as population density increased. Figures 3 and 4 show that the asymptote had not been reached at the highest density in either experiment.

Table 9. The effects of plant population densities and cultivars on the yield components of snap beans.  
Experiment 1, 1972.

Cultivar	% <sup>z</sup> ≥ 4	ln (Racemes/Plant)	Pods/Raceme	Dry Wt. (g)/Pod
OSU 1604	58	1.68	1.65	0.843
OSU 58	71	1.60	1.71	0.978
Gallatin 50	59	1.62	1.61	0.754
L-1	31	1.91	1.63	0.305
Keystone 4672	60	1.69	1.59	0.714
LSD, 5%	--	0.11	ns	0.176
1%	--	0.16	ns	0.255
Population density (plants/m <sup>2</sup> )	% ≥ 4	ln (Racemes/Plant)	Pods/Raceme	Dry Wt. (g)/Pod
91.42	57	1.22	1.46	0.635
76.16	48	1.44	1.49	0.639
63.39	57	1.37	1.65	0.679
43.90	56	1.70	1.54	0.775
36.55	57	1.81	1.76	0.777
30.43	61	2.06	1.81	0.741
21.10	57	2.28	1.74	0.784
LSD, 5%	--	0.16	0.22	0.077
1%	--	0.21	0.29	0.103

<sup>z</sup> Percentage of pods of sieve size 4 or larger.

Table 10. Actual and adjusted<sup>z</sup> effects of plant population densities and cultivars on the yield components of snap beans. Experiment 2, 1972.

Cultivar	<sup>y</sup> %	<u>ln(Racemes/Plant)</u>		<u>Pods/Raceme</u>		<u>Dry Wt. (g)/Pod</u>	
	≥ 4	Actual	Adjusted	Actual	Adjusted	Actual	Adjusted
OSU 1604	76	1.87	1.89	1.89	1.94	0.71	0.68
OSU 58	74	1.80	1.81	1.89	1.92	0.68	0.66
Gallatin 50	65	1.63	1.61	2.07	2.01	0.49	0.53
L-81	73	2.08	2.09	1.66	1.68	0.44	0.43
Keystone 4672	66	2.02	2.01	1.49	1.44	0.45	0.48

Population density (plants/m <sup>2</sup> )	<sup>y</sup> %	<u>ln(Racemes/Plant)</u>		<u>Pods/Raceme</u>		<u>Dry Wt. (g)/Pod</u>	
	≥ 4	Actual	Adjusted	Actual	Adjusted	Actual	Adjusted
109.84	76	1.33	1.35	1.62	1.68	0.56	0.52
91.42	70	1.51	1.51	1.81	1.81	0.53	0.53
76.16	75	1.55	1.57	1.76	1.81	0.60	0.57
63.39	70	1.66	1.65	1.67	1.66	0.59	0.59
52.73	74	1.82	1.83	1.77	1.81	0.58	0.56
43.90	74	1.94	1.95	1.83	1.86	0.56	0.55
36.55	74	2.10	2.11	1.72	1.75	0.60	0.59
30.43	67	2.20	2.18	1.92	1.88	0.53	0.56
25.35	68	2.29	2.29	1.92	1.89	0.54	0.56
21.10	60	2.41	2.38	1.98	1.86	0.49	0.56

<sup>z</sup> Means adjusted to a common maturity by analysis of covariance.

<sup>y</sup> Percentage of pods of sieve size 4 or larger.

Although the cultivar x population density interactions were not statistically significant at the 5% probability levels, the interaction was statistically significant at the 10% level in Experiment 1. The number of racemes per plant of 'L-1' and 'Keystone 4672' decreased at a greater rate as population density increased. The lower optimum population densities of these cultivars could partly be a function of this response.

#### Pods Per Raceme

The number of pods per raceme differed among the cultivars in Experiment 2 (Table 10) but did not differ in Experiment 1 (Table 9). In Experiment 2, the number of pods per raceme of a cultivar was directly related to the size of its leaves. In Experiment 1, the cultivar with the smallest leaves, 'L-1,' did not have significantly fewer pods per raceme. This cultivar was, however, at a very early stage of reproductive development, having only 35% of its pods at sieve size 4 or greater.

As population density increased, a significant linear decline was observed in the number of pods per raceme (Table 11 and Figures 3 and 4). The cultivar x population density interactions were not statistically significant, indicating the rate of decline was approximately the same for all cultivars. Fery and Janick (40) noted a decline in the number of tomatoes per cluster as density increased. They

attributed it to a reduction in the number of flowers to set fruit rather than to a decline in the number of flowers per cluster. They were unable to detect any significant differences among cultivars but showed the decline tended to be less for the compact ones.

As noted earlier, a significant reduction in the number of pods per raceme occurred during the late stages of crop development. This fact is further substantiated by a negative adjustment factor calculated in the analysis of covariance.

#### Average Pod Weight

On a dry weight basis, 'OSU 1604' and 'OSU 58' had the largest pods in both experiments (Tables 9 and 10). The cultivars with small leaves, 'Keystone 4672,' 'L-81' and 'L-1,' tended also to have small pods. This parameter represents the average weight of all the acceptable pods on the plant, therefore, it is influenced by the concentration of pod set. The lower average pod weights of 'Gallatin 50' and 'Keystone 4672' may be partly a manifestation of their less concentrated reproductive developments.

In Experiment 1, the pod size decreased linearly as population density increased (Tables 9 and 11 and Figure 3). In Experiment 2, the relationship between pod size and population density was obscured by differences in sieve size distribution among the densities. Nonetheless, after the data were adjusted to a common sieve size

Table 11. The linear regression analysis<sup>z</sup> of the effects of plant population densities on the yield components of bush snap beans. Experiments 1 and 2, 1972.

X variable	Y variable		
	ln(racemes/plant)	Pods/raceme	dry wt(g)/pod
	ln(plants/m <sup>2</sup> )	plants/m <sup>2</sup>	plants/m <sup>2</sup>
<u>Experiment 1</u>			
$\beta_0$	4.4407	1.8777	0.8424
$\beta_1$	-0.7152	-0.0047	-0.0024
r	0.98**	0.86*	0.93**
r <sup>2</sup>	0.97	0.73	0.87
<u>Experiment 2</u>			
$\beta_0$	4.3561	1.8985	0.5778
$\beta_1$	-0.6388	-0.0018	-0.0004
r	0.99**	0.65*	0.49
r <sup>2</sup>	0.99	0.43	0.24

z Regression equation:  $Y = \beta_0 + \beta_1 X$

\* Significant at the 5% level

\*\* Significant at the 1% level

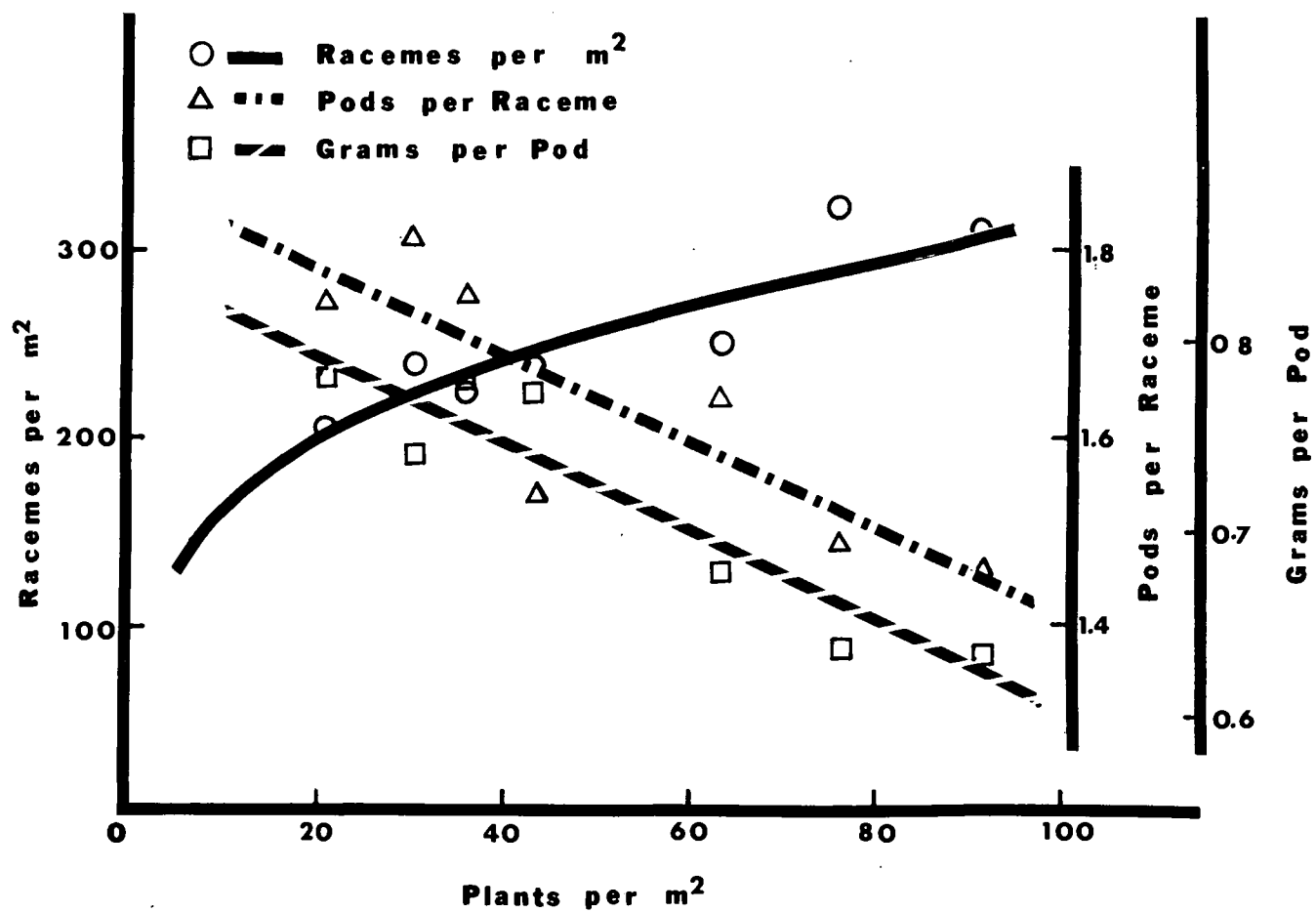


Figure 3. Effect of population densities on the yield components of bush snap beans, as predicted by the regression equations in Table 11. Experiment 1, 1972.



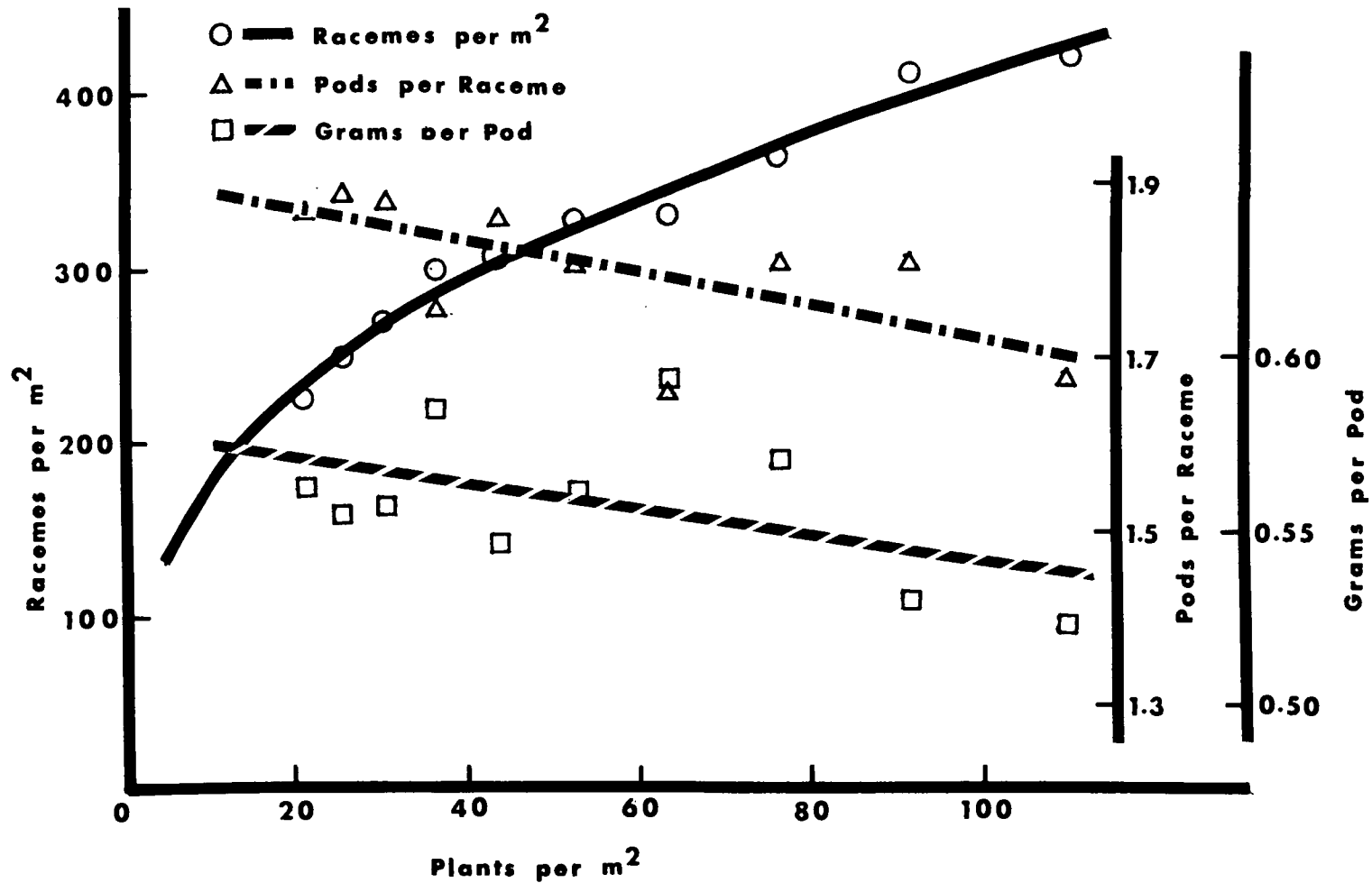


Figure 4. Effect of population densities on the yield components of bush snap beans, as predicted by the regression equations in Table 11. Experiment 2, 1972.

distribution, the pod size tended to decrease linearly as density increased (Tables 10 and 11 and Figure 4). Jones (62) and Mosley (81) have reported similar results. Mosley said the pods were shorter as density increased.

The interaction of cultivar x population density was not statistically significant at the 5% probability level in either experiment.

### Summary

The yield component analysis shows the high yields of 'OSU 1604' and 'OSU 58' were mainly a function of their large average pod size. The small leaved cultivars had greater numbers of racemes per plant, but they also had fewer pods per raceme and smaller pods.

As population density increased, over the range investigated, racemes per area increased asymptotically and the number of pods per raceme and the average pod weight declined linearly. The optimum population density was reached when the number of racemes per area was increasing at a rate only sufficient to compensate for the reductions in pods per raceme and average pod weight (Figures 3 and 4.

The yield component data were generally too variable to explain the differences in the pod yield-population density responses of the cultivars, identified by the modified reciprocal equation.

### Structural Development

Stem length, nodes on the main stem prior to the formation of the terminal inflorescence and branch number were examined in Experiment 2 to characterize the effects of population density and cultivar on structural development.

#### Stem Length

The effect of plant population density on the stem length of snap beans was dependent on the cultivar (Table 12). The stem lengths of 'OSU 1604' and 'OSU 58' increased asymptotically as population density increased, but that of 'Gallatin 50' decreased. The stem lengths of the two smaller leaved cultivars, 'L-81' and 'Keystone 4672,' were not significantly affected by population density. Mosley (81) examined the effect of plant population density on the stem length of 'Gallatin 50.' His results were variable: the stem length increased as density increased in one experiment but showed the opposite response in another experiment. Hicks et al. (49) reported the plant heights of determinate soybean cultivars increased more than those of normal cultivars as density increased.

A significant interaction was found between cultivar and sampling date (Table 13). 'L-81' had significantly longer stems than 'OSU 58,' 'Gallatin 50' and 'Keystone 4672' at the first sampling date but had

Table 12. The ln of stem length (cm) of five snap bean cultivars at seven plant population densities. Experiment 2, 1972.

Population density (plants/m <sup>2</sup> )	Cultivar				
	OSU 1604	OSU 58	Gallatin 50	L-81	Keystone 4672
91.42	3.53	3.37	3.25	3.21	3.23
76.16	3.54	3.36	3.28	3.19	3.21
63.39	3.52	3.38	3.29	3.19	3.25
43.90	3.50	3.35	3.28	3.25	3.21
36.55	3.48	3.34	3.31	3.25	3.24
30.43	3.45	3.33	3.33	3.22	3.19
21.10	3.42	3.28	3.31	3.26	3.19

LSD between two population densities of the same cultivar,

5% = 0.07

1% = 0.09

LSD between two cultivars at the same or different population densities,

5% = 0.11

1% = 0.15

Table 13. The ln of stem length (cm) of five bush snap bean cultivars at four sample dates. Experiment 2, 1972.

Cultivar	Sample number (days from planting)			
	1 (28)	2 (42)	3 (57)	4 (70)
OSU 1604	2.43	3.76	3.88	3.89
OSU 58	2.06	3.62	3.84	3.86
Gallatin 50	1.86	3.45	3.92	3.94
L-81	2.24	3.37	3.64	3.62
Keystone 4672	1.91	3.33	3.78	3.85

LSD of sample x cultivar means, 5% = 0.18

1% = 0.24

significantly shorter stems at the final sample. The two cultivars with a later peak of reproductive development, 'Gallatin 50' and 'Keystone 4672,' had a greater increase in stem length between samples 2 and 3, the two-week period after initial bloom, than the other three cultivars.

### Nodes

No significant differences were found among either cultivars or population densities in the number of nodes forming on the main stems prior to the formation of the terminal inflorescence (Table 14).

Table 14. The number of nodes on the main stem prior to the formation of the terminal inflorescence of bush snap beans. Experiment 2, 1972.

Population density (plants/m <sup>2</sup> )	Nodes	Cultivar	Nodes
91.42	5.9	OSU 1604	6.2
76.16	5.9	OSU 58	5.6
63.39	5.8	Gallatin 50	6.0
43.90	5.8	L-81	5.5
36.55	5.8	Keystone 4672	6.0
30.43	5.9	LSD, 5%	ns
21.10	5.8		
LSD, 5%	ns		

This indicates the differences among the stem lengths of cultivars and population densities were due to differences in the lengths of internodes. These results are consistent with those reported by Hinson

and Hanson (50) for determinate soybeans. On the other hand, a decrease in the total number of nodes has been observed on indeterminate plants (51, 47).

### Branch Development

Branch development began after sample 1, taken 27 days after planting. Differences were found among the cultivars (Table 15). The cultivars that had early development of reproductive sink ceased branch development by sample 3, but branch development continued on the cultivars with poor initial reproductive development. Regardless of the sample date, the cultivars with smaller leaves had greater numbers of branches.

Few branches developed on the plants at the high population densities. As population density increased, the number of branches per area increased toward a peak level and then declined. A significant cultivar x population density interaction was found (Table 16). Cultivars with smaller leaves reached their peak numbers of branches per area at higher population densities. This response could indicate deeper penetration of light into the foliar canopies of these cultivars. Hodgson and Blackman (51) stated that reduced branch development at higher densities was caused by lower light intensities toward the bottom of the crop canopies. Studies comparing soybean cultivars

have shown that narrow leaves allowed light to penetrate deeper into the crop canopies.

Table 15. The branches per area ( $m^2$ ) of five bush snap bean cultivars at three sample dates. Experiment 2, 1972.

Cultivar	Sample number (days from planting)		
	2 (42)	3 (57)	4 (70)
OSU 1604	67.8	116.3	100.1
OSU 58	73.6	123.2	111.9
Gallatin 50	45.5	103.1	119.9
L-81	160.8	207.6	207.2
Keystone 4672	144.3	207.6	257.2
LSD of Sample x Cultivar means, 5% = 24.3 1% = 32.8			

Table 16. The branches per area ( $m^2$ ) of five bush snap bean cultivars at seven population densities. Experiment 2, 1972.

Population density (plants/ $m^2$ )	Cultivar				
	OSU 1604	OSU 58	Gallatin 50	L-81	Keystone 4672
91.42	50.8	90.4	60.9	229.6	242.8
76.16	83.8	102.4	66.9	231.9	255.6
63.39	98.6	119.0	88.7	226.1	220.5
43.90	118.5	113.7	105.4	186.8	204.4
36.55	118.2	106.0	113.7	169.3	197.0
30.43	104.8	97.7	101.8	166.0	165.3
21.10	88.4	91.2	89.1	133.4	136.0

LSD between two population densities of the same cultivar,  
5% = 27.9  
1% = 36.8

LSD between two cultivars at the same or different population densities, 5% = 29.4  
1% = 39.0

The cultivars having higher optimum population densities for branch development also had higher optimum population densities for pod yields. Studies have shown that cultivars with an inherently greater number of branches tended to reach peak yields at higher densities (40, 50).

The number of branches per plant declined at a greater rate than the number of racemes per plant. This suggests a greater percentage of the racemes were borne in the axils of leaves on the main stems as density increased. Jones (62) made a similar observation.

#### Leaf Area and Leaf Area Components

The results of the statistical analyses of leaf area and leaf area components, i. e. leaf number and area per leaf, have been summarized in Table 17.

#### Leaf Area

The cultivars had different patterns of foliar development (Table 18). 'OSU 1604' and 'OSU 58' had slightly greater leaf areas than either 'Gallatin 50,' 'Keystone 4672' or 'L-81' prior to bloom, but lower leaf areas during the period of reproductive development. The leaf areas of the 'OSU' cultivars did not increase after the start of reproductive development. Those of the other cultivars did. The



Table 17. Analysis of variance for ln of leaf area (cm<sup>2</sup>) per plant, ln of leaf number per plant and average area (cm<sup>2</sup>) per leaf. Experiment 2, 1972.

Source of Variation	D. F.	Mean squares		
		Leaf area	Leaf number	Area per leaf
Sample date	3	34.46**	121.2**	29973**
Cultivar	4	.06876**	.05922**	40248**
Sample x Cultivar	12	12.32**	.01003**	1409**
Error (a)	38	.02476	.01633	512
Population density	6	78.83**	44.98**	2885**
Sample x Population	18	35.04**	.04737**	205.2**
Cultivar x Population	24	.04506	.04862**	84.5
Sample x Cultivar x Population	72	.04079	.03495*	89.3
Error (b)	240	.03629	.02425	97.1

\* p < .05

\*\* p < .01

total leaf areas of all cultivars declined between samples 3 and 4, but the loss of the 'OSU' cultivars was proportionately greater.

Table 18. The ln of leaf area per plant ( $\text{cm}^2$ ) of five snap bean cultivars at four sampling dates. Experiment 2, 1972.

Cultivar	Sample number (days from planting)			
	1 (28)	2 (42)	3 (57)	4 (70)
OSU 1604	5.59	6.56	6.70	5.67
OSU 58	5.55	6.51	6.56	6.17
Gallatin 50	5.35	6.40	6.91	6.68
L-81	5.36	6.45	6.77	6.41
Keystone 4672	5.34	6.48	6.89	6.64
LSD of sample x cultivar means, 5% = 0.31				
1% = 0.42				

Leaf area per plant declined as population density increased. The cultivar x population density interaction was not significant indicating the rate of decline was approximately the same for all cultivars (Table 17). When the natural logarithms of leaf area per plant were plotted against the natural logarithms of population density, linear relationships were revealed (Figure 5). The differences in the slopes of the lines for the different samples illustrate the nature of the population density x sample date interaction. The rate of increase in leaf area, between samples 1 and 2, was greater at lower plant densities. Conversely, the decrease in leaf area between samples 3 and 4 was proportionally greater at the higher densities. Weber et al. (117) reported a similar response for soybeans.

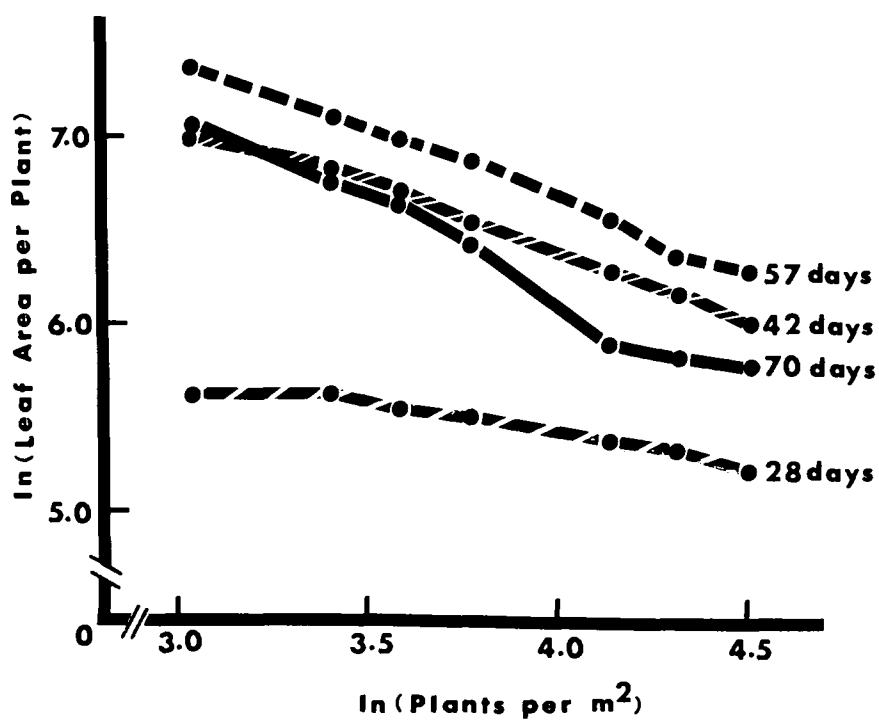


Figure 5. Effect of population densities on the leaf area per plant of bush snap beans at four sample dates (days from planting). Experiment 2, 1972.

The leaf area index (LAI) increased asymptotically as population density increased (Figure 6). At sample 3, the LAI was still increasing at the highest density investigated. At the final sample, LAI was virtually the same across the entire range of densities, because of the proportionally greater loss of leaf area at the higher densities. The maximum LAI recorded was approximately 5.5, for the highest population density of 'Gallatin 50' at sample 3. Mosley (81) recorded an LAI as high as 8 for the same cultivar. In addition, Weber et al. (117) reported LAI as high as 8 for soybeans. The lower levels of LAI for the present study may have resulted from the exclusion of apparently nonfunctional leaves in the leaf area determinations. A critical LAI of 4 has been reported for snap beans (62) and soybeans (26, 96). Table 19 shows only two cultivars, 'Gallatin 50' and 'Keystone 4672,' growing at the highest densities, were able to maintain an LAI of 4 during the period of reproductive development. These cultivars had the lowest pod yields.

In order to measure the relative potentials of assimilate sources and sinks, the ratios of leaf area to raceme and branch number were calculated (Table 20). During the period prior to bloom, the leaf area per branch was greater at higher densities. After the start of reproductive development, the leaf area per raceme was greater at the lower densities. These results suggest the leaves of the plants at

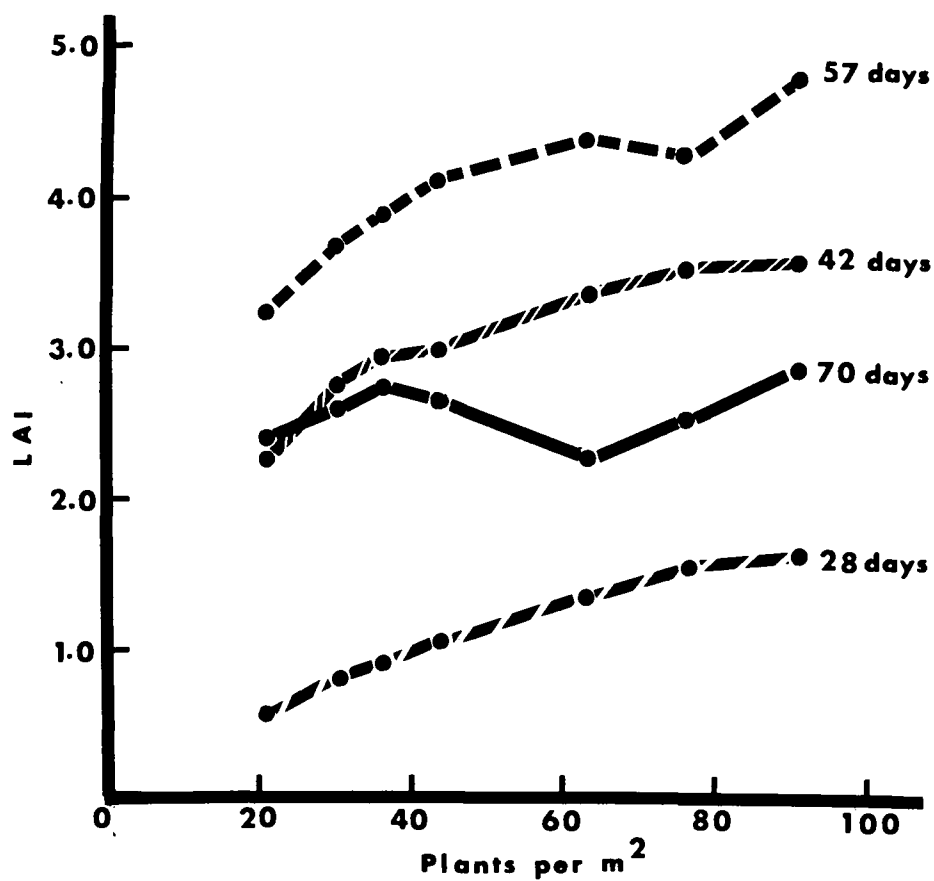


Figure 6. Effect of population densities on the leaf area index of bush snap beans at four sample dates (days from planting). Experiment 2, 1972.

Table 19. The effect of plant population densities on the mean leaf area index (LAI) of bush snap beans during three time periods. Experiment 2, 1972.

Cultivar	Days from Planting	Population density (plants/m <sup>2</sup> )								Cultivar means
		91.42	76.16	63.39	43.90	36.55	30.43	21.10		
OSU 1604	28-42	2.78	2.75	2.33	2.15	1.97	1.76	1.33	2.15	
	42-57	4.12	3.85	3.60	3.60	3.49	3.22	2.80	3.53	
	57-70	2.85	2.21	1.78	2.39	2.63	2.37	2.41	2.38	
OSU 58	28-42	2.53	2.34	2.40	2.12	1.87	1.73	1.34	2.05	
	42-57	3.48	3.38	3.77	3.41	3.10	2.90	2.52	3.22	
	57-70	3.12	2.98	3.03	2.66	2.53	2.61	2.27	2.74	
Gallatin 50	28-42	2.28	2.11	1.97	1.71	1.61	1.51	1.23	1.77	
	42-57	4.31	3.94	3.65	3.76	3.60	3.36	3.08	3.67	
	57-70	4.88	4.15	4.24	4.23	4.23	3.94	3.54	4.17	
L-81	28-42	2.24	2.28	2.02	1.79	1.60	1.51	1.24	1.81	
	42-57	4.11	4.04	4.04	3.37	3.30	3.06	2.56	3.50	
	57-70	3.62	3.51	3.83	3.58	3.48	3.13	2.85	3.43	
Keystone 4672	28-42	2.53	2.50	2.32	1.60	1.65	1.49	1.07	1.88	
	42-57	4.84	4.30	4.12	3.52	3.59	3.49	2.71	3.79	
	57-70	4.65	4.39	4.00	4.31	4.03	3.80	3.12	4.04	
Population means	28-42	2.47	2.39	2.21	1.87	1.74	1.60	1.24		
	42-57	4.17	3.90	3.84	3.53	3.42	3.21	2.74		
	57-70	3.82	3.45	3.38	3.43	3.38	3.17	2.84		

higher densities had a lesser sink demand prior to bloom, but a greater sink demand after bloom.

Table 20. The effect of plant population densities on the leaf area ( $\text{cm}^2$ ) per branch and the leaf area per raceme of bush snap beans. Experiment 2, 1972.

Population density (plants/ $\text{m}^2$ )	Sample number (days from planting)		
	2(42) leaf area per branch	3(57) leaf area per raceme	4(70) leaf area per raceme
91.42	397.7	132.8	75.3
76.16	322.3	146.6	78.0
63.39	308.2	151.5	81.3
43.90	290.4	163.0	92.0
36.55	282.6	173.3	95.4
30.43	279.8	195.1	98.4
21.10	297.9	197.1	103.9

#### Area Per Leaf

The cultivars used in these studies were selected partly because of purported differences in the sizes of their leaves. As expected, the leaves of 'L-81' and 'Keystone 4672' were significantly smaller than those of 'OSU 1604,' 'OSU 58' and 'Gallatin 50' (Table 21).

'L-81' had slightly smaller leaves than 'Keystone 4672.'

A significant cultivar x sampling date interaction was found (Table 17). The leaf sizes of all cultivars increased significantly between samples 1 and 2, but after sample 2, the leaf size of 'Gallatin 50' continued to increase, while the leaf sizes of the other cultivars

did not (Table 21). As a result, 'Gallatin 50' had the largest leaves at the final sample.

Table 21. The area per leaf ( $\text{cm}^2$ ) of five snap bean cultivars at four sampling dates. Experiment 2, 1972.

Cultivar	Sample number (days from planting)			
	1 (28)	2 (42)	3 (57)	4 (70)
OSU 1604	65.0	109.3	102.1	108.6
OSU 58	65.0	110.5	106.4	102.3
Gallatin 50	59.6	108.3	122.0	125.5
L-81	43.7	61.7	66.0	69.5
Keystone 4672	47.2	77.2	77.4	79.9
LSD of Sample x Cultivar means, 5% = 14.2 1% = 19.0				

Although, the average area of a leaf was inversely related to plant population density at all sample dates, a significant population density x sample date interaction was found (Table 22). Between samples 1 and 2, the average leaf size increased approximately 66% for all population densities. After sample 2, the leaf sizes continued to increase at the higher densities but remained relatively constant at the lower ones. As a result, the differences in leaf sizes among the population densities decreased toward the later stages of crop development. The reduction in leaf size as density increased, agrees with the results of Mosley (81).



Table 22. The area per leaf ( $\text{cm}^2$ ) of snap beans at seven plant population densities and four sampling dates. Experiment 2, 1972.

Population density (plants/ $\text{m}^2$ )	Sample number (days from planting)			
	1 (28)	2 (42)	3 (57)	4 (70)
91.42	46.4	79.2	87.3	94.6
76.16	50.2	84.8	86.1	91.8
63.39	53.4	85.0	90.3	96.5
43.90	57.8	94.8	94.7	92.1
36.55	58.9	100.2	97.4	103.6
30.43	63.3	101.0	101.9	97.9
21.10	62.5	108.8	105.9	103.4

LSD between two population densities at the same sampling date,

5% = 7.1

1% = 9.3

LSD between two sampling dates at the same or different population densities, 5% = 9.1

1% = 12.1

### Leaf Number

The analysis of leaf number per plant revealed that all main effects and interactions, including the second order interaction of sample date x cultivar x population density, were statistically significant (Table 17). The common trend shown by all cultivars and population densities was for leaf number per plant to increase up to the sample 3 and then to decline between samples 3 and 4 (Table 22 and Figure 7). An almost complete senescence of the leaves of 'OSU 1604,' growing at high densities, was responsible for the second order interaction.

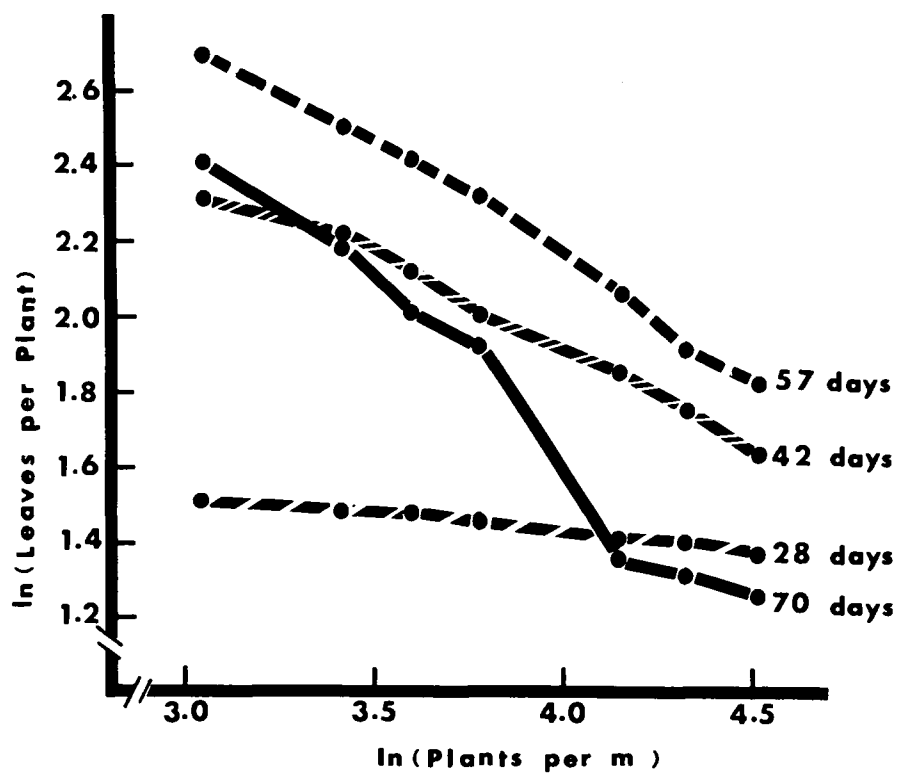


Figure 7. Effect of population densities on the leaf number per plant of bush snap beans at four sample dates (days from planting). Experiment 2, 1972.

The differences in leaf number among the cultivars and the population densities were relatively small at sample 1. Later in the season, after a period of branch development, the differences among the treatments increased.

The leaf number of a cultivar was inversely related to its leaf size (Table 23). In addition, the leaf number of a cultivar was influenced by its pattern of reproductive development. The two 'OSU' cultivars produced the fewest leaves during the period of initial reproductive development. The 'OSU' cultivars also lost a proportionally greater number of leaves between samples 3 and 4.

Table 23. The ln of leaf number per plant of five snap bean cultivars at four sampling dates. Experiment 2, 1972.

Cultivar	Sample number (days from planting)			
	1 (28)	2 (42)	3 (57)	4 (70)
OSU 1604	1.43	1.87	2.08	1.02
OSU 58	1.39	1.82	1.91	1.55
Gallatin 50	1.30	1.76	2.11	1.86
L-81	1.59	2.35	2.59	2.19
Keystone 4672	1.51	2.14	2.55	2.26
LSD of sample x cultivar means, 5% = 0.25				
1% = 0.34				

The natural logarithm of leaf number was linearly related to the natural logarithm of population density (Figure 7). Between samples 1 and 2, the increase in leaf number was greater at the lower

densities. Conversely, between samples 3 and 4, the decline in leaf number was proportionally greater at the higher densities. Weber et al. (117) have recorded a similar population density x sample date interaction for soybeans. Mosley (81) found, however, the leaf number per plant continued to increase at the lower densities up to marketable harvest. At the higher densities, he found the leaf number stopped increasing prior to harvest.

### Summary

Among cultivars, the patterns of leaf area development were related to the patterns of reproductive development. The cultivars having a relatively early and rapid reproductive development, 'OSU 1604' and 'OSU 58,' had an earlier cessation of leaf area development and a more precipitous decline in leaf area between samples 3 and 4. At the onset of reproductive development, all five cultivars had approximately the same leaf areas. Afterwards, 'OSU 1604' and 'OSU 58' had significantly lower leaf areas, but they produced higher pod yields. In fact, the pod yields of the cultivars were inversely related to their leaf areas during reproductive development. This relationship occurred because the higher leaf areas of 'Gallatin 50' and 'Keystone 4672' were either a manifestation of greater competition between vegetative and reproductive growth or a result of compensatory foliar development for inadequate reproductive development.

During early development, the leaf area of a cultivar was directly related to the size of its leaves. Later in the season, after a period of branch development, cultivars with smaller leaves compensated by producing greater numbers of leaves. Nevertheless, the lower leaf areas of the small-leaved cultivar could reduce the growth rates of the young plants.

The LAI increased asymptotically as population density increased. Between samples 1 and 2, the lower densities had a proportionally greater increase in leaf area per plant. Therefore, the higher densities had a relatively older average leaf age. The greater decline in leaf area at the higher densities between samples 3 and 4 could be related to the older leaves. It also could have resulted from an inadequate supply of an essential growth factor, such as water or mineral nutrients. The reductions in the number of pods per raceme and the average pod size at increased densities may be a function of this older average leaf age and greater decline in leaf area. It could also be a result of the smaller leaf area per raceme found at the higher densities.

The effect of plant population density on the ratio of leaf area to sink potential depended on the stage of crop development. Prior to bloom, assuming the sink potential was related to branch number, the ratio of leaf area to sink was higher at the higher densities.

After bloom, assuming the sink potential was related to the number of racemes, the ratio of leaf area to sink was higher at the lower densities.

### Foliar Efficiency

#### Leaf Area Ratio

The statistical analysis of leaf area ratios (LAR) is summarized in Table 24. The LAR of all cultivars declined as crop development progressed (Table 25). A similar decline was reported by Wallace *et al.* (108). The differences in LAR among the cultivars were relatively small at samples 1 and 2. The decline in LAR from sample 1 to sample 2 was slight. After sample 2, the decline in LAR of a cultivar was directly related to the intensity of its reproductive development. The LAR of the two 'OSU' cultivars and 'L-81' declined precipitously between samples 2 and 3, but the LAR of 'Gallatin 50' and 'Keystone 4672' declined slightly. Between samples 3 and 4, all cultivars showed a great reduction in LAR.

Wallace and Munger (106) compared several dry bean cultivars and found the yields were highly and positively correlated with the LAR. On the other hand, Buttery and Buzzell (27) reported a negative relationship between the grain yields of soybean cultivars and their LAR values. The results of the present study agree with those of

Table 24. Analysis of variance for Leaf Area Ratio (LAR) and Specific Leaf Area (SLA). Experiment 2, 1972.

Source of Variation	D. F.	Mean Squares	
		LAR	SLA
Sample date	3	178275**	90921**
Cultivar	4	10324**	3755
Sample x Cultivar	12	1516**	2593
Error(a)	38	273	2283
Population density	6	157**	10030**
Sample x Population	18	175**	1343
Cultivar x Population	24	45	1009
Sample x Cultivar x Population	72	47	853
Error (b)	240	41	834

\*  $p < .05$

\*\*  $p < .01$

Table 25. The effects of plant population densities and cultivars on the leaf area ratio (LAR) of snap beans at four sampling dates. Experiment 2, 1972.

Cultivar	Sample number (days from planting)			
	1 (28)	2 (42)	3 (57)	4 (70)
OSU 1604	133.7	114.0	65.7	22.2
OSU 58	125.7	113.2	65.7	33.6
Gallatin 50	140.2	127.3	110.0	55.6
L-81	136.0	131.0	85.1	45.3
Keystone 4672	132.0	124.7	102.0	54.0

LSD of Sample x Cultivar means, 5% = 10.3

1% = 13.8

<u>Plants/m<sup>2</sup></u>				
91.42	139.4	128.4	85.5	39.3
76.16	137.8	123.1	87.0	38.4
63.39	134.8	123.5	86.4	40.6
43.90	133.8	122.6	86.5	41.9
36.55	131.9	121.7	84.7	44.0
30.43	130.0	119.4	87.5	44.5
21.10	126.8	115.7	82.4	46.2

LSD between two population densities at the same sampling date,

5% = 4.6

1% = 6.1

LSD between two sampling dates at the same or different population densities, 5% = 19.8

1% = 26.3



Buttery and Buzzell. The cultivars producing the highest pod yields had the lowest LAR values during the period of reproductive development. The relatively high LAR of 'Gallatin 50' and 'Keystone 4672,' the poor yielding cultivars, were due either to competition or to a compensatory relationship between foliar and reproductive development. Prior to the onset of reproductive development, the LAR values were approximately the same for all cultivars.

A significant sample date x population density interaction was found (Table 24). The LAR increased slightly with increasing population density at samples 1 and 2; it was not affected by density at sample 3; it declined slightly with increasing population density at sample 4 (Table 25). The negative relationship at sample 4 was probably a result of a proportionally greater senescence of leaves at the higher densities. Other studies have shown LAR to be negatively related to population density and LAI.

### Specific Leaf Area

The statistical analysis of specific leaf area (SLA) has been summarized in Table 24. The value of 'F' for the interaction of plant density and sampling date missed significance at the 5% level of probability by less than 0.02. It was significant at the 10% level.

The SLA increased considerably for all cultivars and population densities between samples 1 and 2; thereafter, it remained relatively

constant (Table 26 and Figure 8). Eastin and Gritton (36) reported a similar response for peas (Pisum sativum L.).

The SLA increased as population density increased at samples 1 and 2 (Figure 8). At the later samples, the SLA tended toward a constant value over an increasing range of population densities. These results are generally consistent with the proposal that SLA is directly related to the degree of mutual shading resulting from increasing LAI.

'OSU 1604' and 'OSU 58' tended to have lower SLA than the other cultivars, especially during the period prior to reproductive development (Table 26). This result is in accordance with the observation of Buttery and Buzzell (27) that selection for higher soybean yields had concomitantly increased SLW (decreased SLA). They suggested using this parameter as a selection criterion.

Table 26. The effects of cultivars and sample dates on the specific leaf areas (SLA)<sup>z</sup> of bush snap beans. Experiment 2, 1972.

Cultivar	Sample number (days from planting)				Cultivar means
	1 (28)	2 (42)	3 (57)	4 (70)	
OSU 1604	193.7	232.6	218.8	268.1	228.3
OSU 58	182.0	235.8	239.5	250.0	226.8
Gallatin 50	195.5	254.2	259.4	262.9	243.0
L-81	197.9	257.6	241.6	240.2	234.3
Keystone 4672	184.7	253.3	253.2	259.8	237.8
Sample means	190.7	246.7	242.5	256.2	

<sup>z</sup>Specific leaf area calculated as leaf area (cm<sup>2</sup>)/leaf weight (grams).

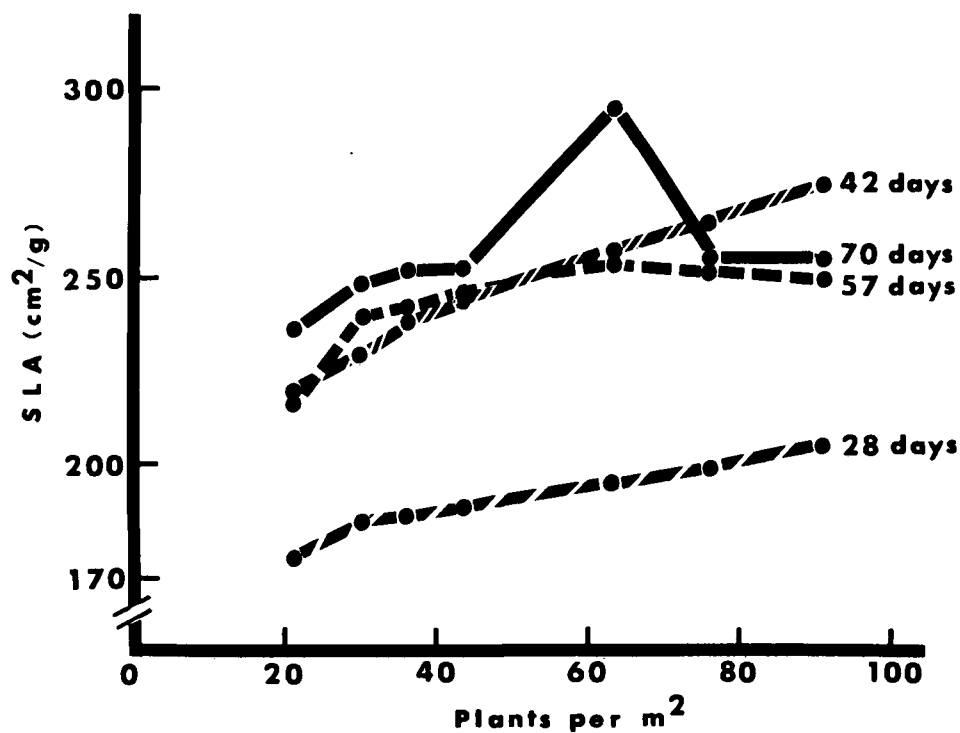


Figure 8. Effect of population densities on the specific leaf area (leaf area per leaf dry weight) of bush snap beans at four sample dates (days from planting). Experiment 2, 1972.

### Net Assimilation Rate

Net assimilation rates (NAR) were calculated, using the mean total dry weights and leaf areas from the three replications. The data have not been statistically analyzed.

The relative NAR of the cultivars depended on the stage of crop development (Table 27). During the prebloom period, between samples 1 and 2, the NAR of 'OSU 1604,' 'OSU 58' and 'Keystone 4672' were greater than those of 'Gallatin 50' and 'L-81.' The NAR of all cultivars were lower during the second sample period; however, the reductions were less for the cultivars with a rapid development of reproductive sink: 'OSU 1604,' 'OSU 58' and 'L-81.' The NAR of the cultivars with later reproductive development, 'Gallatin 50' and 'Keystone 4672,' increased for the last sample period, but the NAR of the other three either declined or increased, but slightly.

These results show that reproductive development has a positive effect on the net photosynthetic efficiency of leaves. A similar relationship has been reported by Wallace and Munger (106). They found a general decline in NAR as the season progressed, but noted an increase in NAR for certain cultivars during initial reproductive development. Hormones being produced by the developing embryos could be increasing the efficiencies of the leaves (59, 95).

Table 27. The effect of plant population densities on the net assimilation rates (NAR)<sup>2</sup> of five snap bean cultivars during three time periods. Experiment 2, 1972.

Cultivar	Days from Planting	Population density (plants/m <sup>2</sup> )							Cultivar means
		91.42	76.16	63.39	43.90	36.55	30.43	21.10	
OSU 1604	28-42	48.72	43.84	62.01	71.27	78.41	78.43	86.11	66.97
	42-57	58.00	48.59	45.57	51.00	48.09	51.01	73.05	53.62
	57-70	25.66	108.70	61.97	41.69	52.40	47.99	14.88	50.47
OSU 58	28-42	43.77	58.94	51.52	72.81	70.23	66.91	91.04	65.03
	42-57	43.01	42.48	52.62	37.67	41.93	48.67	55.40	45.97
	57-70	81.79	56.31	24.95	44.77	41.36	48.93	28.27	46.63
Gallatin 50	28-42	45.83	58.74	44.19	57.80	70.95	74.64	88.51	62.95
	42-57	35.17	26.11	40.65	43.24	37.38	32.98	37.46	36.14
	57-70	50.22	52.40	42.98	43.59	41.03	47.65	39.59	45.35
L-81	28-42	46.61	52.11	59.52	53.25	61.58	70.56	82.06	60.81
	42-57	60.62	46.32	48.27	48.10	54.18	39.55	39.55	48.08
	57-70	18.38	17.40	23.40	54.76	31.48	41.05	52.13	34.09
Keystone 4672	28-42	51.68	54.10	59.55	60.81	73.44	84.51	88.70	67.54
	42-57	37.13	22.33	24.61	46.37	38.97	33.71	47.52	35.81
	57-70	32.41	64.85	35.73	42.47	44.48	33.36	22.50	39.40
Population means	28-42	47.32	53.55	55.36	63.19	70.92	75.01	87.28	
	42-57	46.79	37.17	42.34	45.28	44.11	41.18	50.60	
	57-70	41.69	59.93	37.81	45.46	42.15	43.80	31.47	

<sup>2</sup> NAR expressed as mg of dry weight gained per dm<sup>2</sup> of leaf area per day.

The relationship between  $NAR$  and plant population density also was a function of the stage of crop development (Table 27). During the prebloom period, the  $NAR$  decreased exponentially as population density increased. The  $NAR$  was not influenced by the population density during the periods of reproductive development.

In Figure 9 the  $NAR$  of each population density has been plotted against the corresponding LAI. During the prebloom period, the  $NAR$  declined linearly as LAI increased. During the two subsequent sample periods, when reproductive development was occurring, the  $NAR$  was not significantly influenced by LAI. This lack of correlation during reproductive development could be a result of the lower sink potential at the lower densities, i. e. lower LAI. Previous results have shown a greater leaf area per raceme at the lower population densities (Table 20).

The  $NAR$  values were generally consistent with those previously reported for Phaseolus vulgaris L. (81, 106). Working with soybeans, Buttery and Buzzell (27) calculated  $NAR$  values of 59 mg per dm<sup>2</sup> per day at a LAI of 1 and 35 mg per dm<sup>2</sup> per day at a LAI of 4.

The  $NAR$ -LAI relationships of the cultivars were compared to determine the relative efficiencies of their canopies and leaves (Figure 10). To eliminate the confounding effect of reproductive development, only the data from the prebloom period were analyzed.

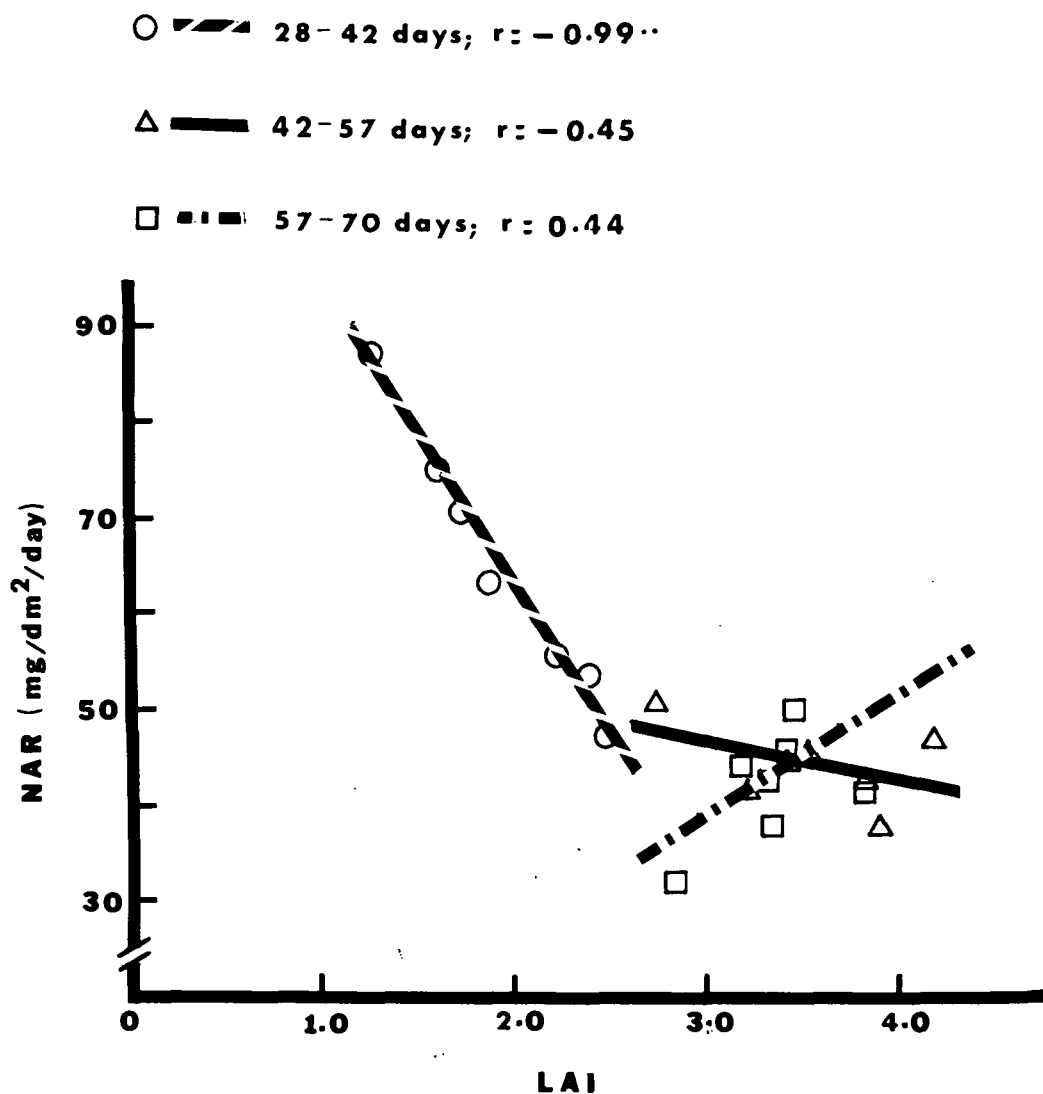


Figure 9. Relationship between net assimilation rates and leaf area indices of bush snap beans during three sample periods. Values represent the mean of five cultivars. Experiment 2, 1972.

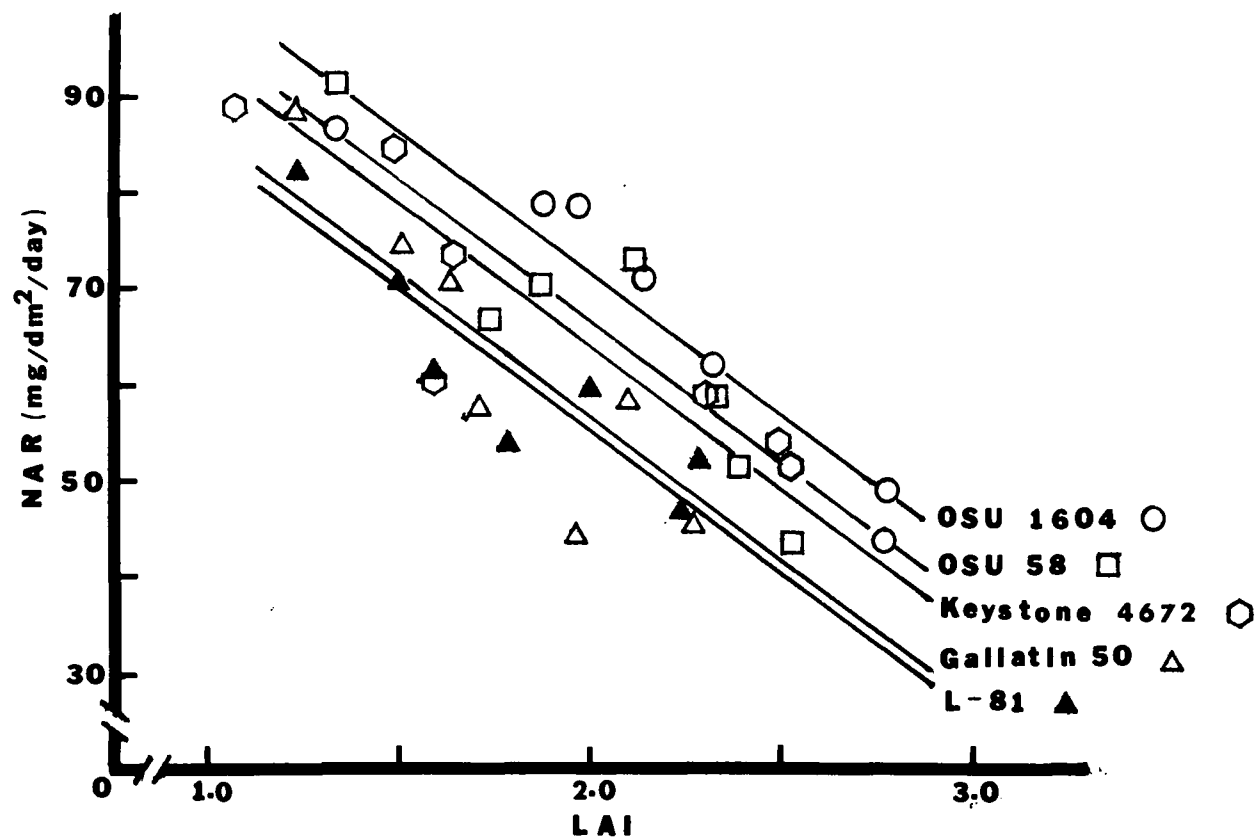


Figure 10. A comparison of the effects of LAI on the NAR of five bush snap bean cultivars during a prebloom sample period. Experiment 2, 1972.



When the linear regression lines were compared by analysis of covariance, no significant differences were found among their slopes; however, significant differences were found in their elevations.

Comparison of Regression Lines

Source	Reg. Coef.	D. F.	Residual M. S.	F
Cultivar				
OSU 1604	29.54	5	0.0220	
OSU 58	33.45	5	0.0450	
Gallatin 50	39.63	5	0.0590	
L-81	28.07	5	0.0340	
Keystone 4672	23.41	5	0.0050	
		<u>25</u>	<u>0.0420</u>	
Cultivar Pooled	29.39	29	0.0420	
Difference Between Slopes		4	0.0430	1.0238 ns
Difference Between Adjusted means		4	0.2996	7.1333 **

The invariance of the slopes indicates that any differences in canopy architecture among the five cultivars did not have an appreciable effect on assimilatory efficiencies of the canopies at increasing levels of LAI. Examination of the differences in the elevations reveals the leaves of the two cultivars having the greatest pod yields, 'OSU 1604' and 'OSU 58,' were more efficient assimilators of dry matter.

The data from samples 1 and 2 were used to determine the relationships between the NAR of the cultivars and their LAR and SLA (Table 28). The cultivars with the higher LAR or SLA tended to have

lower NAR; however, the correlation coefficients were not statistically significant at the 5% level of probability.

Table 28. The relationships between the net assimilation rates (NAR) and the mean leaf area ratios ( $\overline{\text{LAR}}$ ) and mean specific leaf areas ( $\overline{\text{SLA}}$ ) of five bush snap bean cultivars. Experiment 2, 1972.

Cultivar	NAR	$\overline{\text{SLA}}^z$	$\overline{\text{LAR}}^y$
OSU 1604	66.97	213.14	123.81
OSU 58	65.03	208.89	119.46
Gallatin 50	62.95	224.81	133.79
L-81	60.81	227.76	133.52
Keystone 4672	67.54	219.03	128.33

Correlation coefficients:

$\overline{\text{SLA}}$  vs NAR,  $r = -0.69$  ns

$\overline{\text{LAR}}$  vs NAR,  $r = -0.62$  ns

$\overline{\text{SLA}}$  vs  $\overline{\text{LAR}}$ ,  $r = 0.99$  \*\*

$$^z\overline{\text{SLA}} = (\text{SLA}_1 + \text{SLA}_2)/2$$

$$^y\overline{\text{LAR}} = (\text{LAR}_1 + \text{LAR}_2)/2$$

A negative relationship between  $\overline{\text{LAR}}$  and NAR is in accordance with previous experimental results (27, 36). It has been attributed to a greater mutual shading of the leaves of cultivars with higher  $\overline{\text{LAR}}$ . For this experiment, however, the mutual shading explanation is unacceptable because the cultivars having higher  $\overline{\text{LAR}}$  also had lower LAI. A more plausible explanation has been offered by Buttery and Buzzell (27). They said the leaves of plants with a lower  $\overline{\text{LAR}}$

had a higher NAR because there was a relatively larger sink potential for their photosynthetic products.

The negative correlation between NAR and SLA, is consistent with previous observations on soybeans (27, 34). Dornhoff and Shibles (34) attributed the relationship to a lower mesophyll resistance to CO<sub>2</sub> entry at lower SLA, because of a higher cell surface to volume ratio within the leaf.

### Crop Growth

#### Total Dry Weight

The statistical analysis of total dry weights per plant revealed all main effects as well as the population density x sample date interaction were significant (Table 29). The total dry weight per area approached an asymptote as population density increased; however, an interim ceiling yield was not attained by any density at any sample date (Figure 11).

The population density x sample date interaction is illustrated in Figure 12 by plotting the relative growth rates (RGR) against population density. During the period between samples 1 and 2, the RGR declined exponentially as population density increased. This relationship indicates a lower level of interplant competition, existed at the lower population densities. During the two subsequent sample

Table 29. The ln of total above ground dry weight (grams) per plant of bush snap beans. Experiment 2, 1972.

Cultivar	Sample number (days from planting)				Cultivar means
	1 (28)	2 (42)	3 (57)	4 (70)	
OSU 1604	0.695	1.825	2.517	2.748	1.946
OSU 58	0.715	1.787	2.383	2.680	1.892
Gallatin 50	0.414	1.565	2.214	2.675	1.717
L-81	0.445	1.573	2.333	2.625	1.744
Keystone 4672	0.463	1.658	2.265	2.660	1.762

LSD of cultivar means, 5% = 0.086

1% = 0.115

Population  
density  
(plants/m<sup>2</sup>)

91.42	0.240	1.118	1.836	2.161	--
76.16	0.368	1.333	1.891	2.312	--
63.39	0.464	1.453	2.098	2.380	--
43.90	0.597	1.713	2.413	2.748	--
36.55	0.646	1.889	2.557	2.901	--
30.43	0.735	2.031	2.650	3.013	--
21.10	0.775	2.235	2.953	3.230	--

LSD between two population densities at the same sample date,

5% = 0.091

1% = 0.120

LSD between two sample dates at the same or different population densities, 5% = 0.114

1% = 0.155

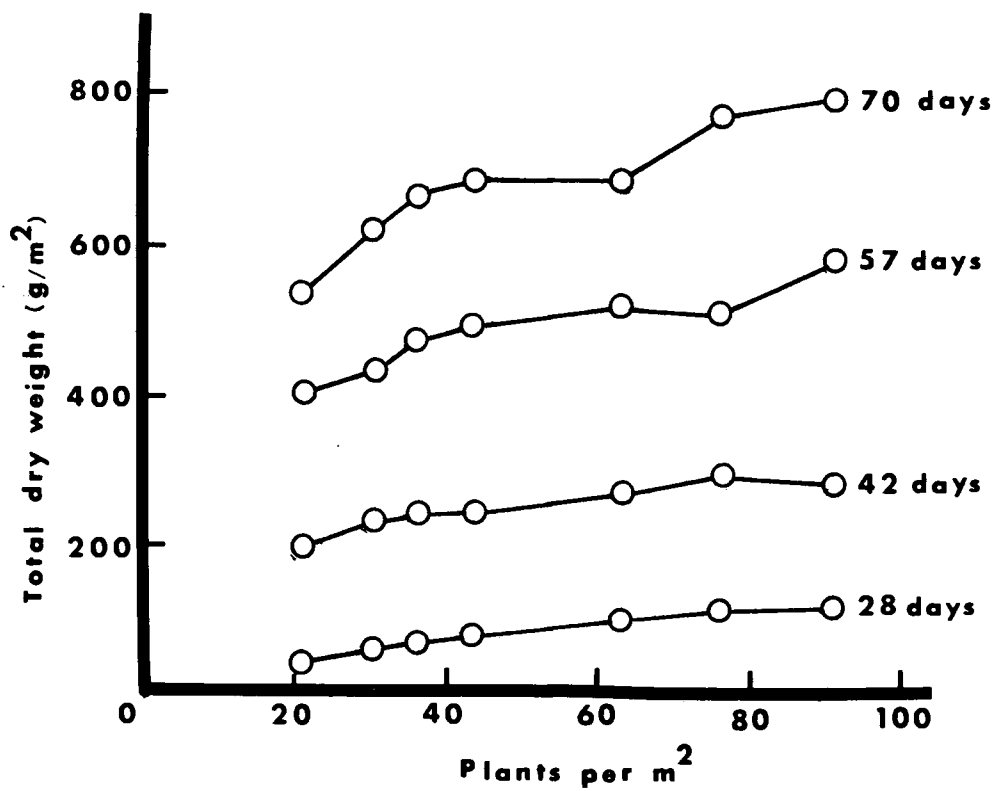


Figure 11. Effect of population densities on the total above ground dry weight per area of bush snap beans at four sampling dates. Experiment 2, 1972.

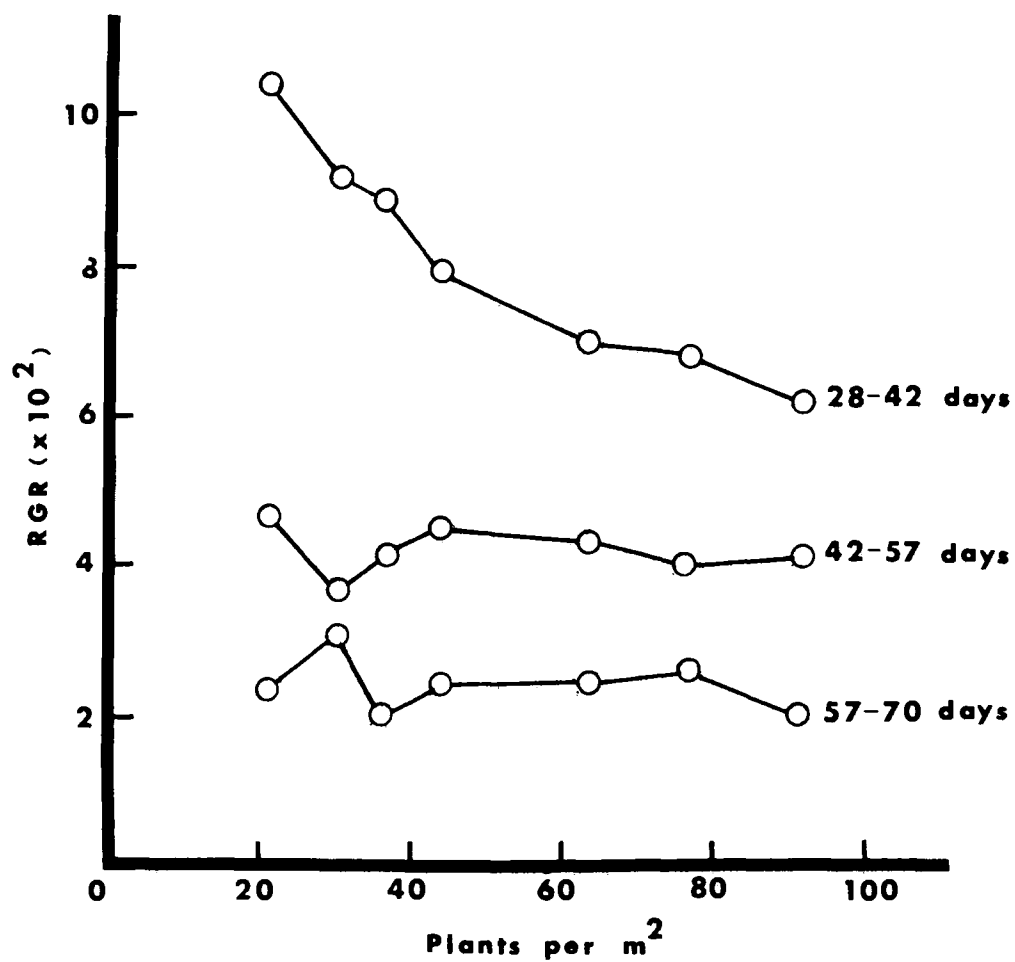


Figure 12. Effect of population density on the relative growth rates of bush snap beans during three sample periods (days from planting). Experiment 2, 1972.

periods, the RGR was constant over the entire range of densities. This ostensibly suggests the level of interplant competition was at the same intensity for all densities.

The relationship between RGR and population density over the course of crop development appears to agree with the theoretical relationship proposed by Bleasdale (10); however, an important discrepancy exists. Bleasdale related the population densities having a common RGR to the range of densities attaining an interim ceiling yield. In the present study, the RGR was constant across the entire range of densities after sample 2 but the interim ceiling yields were not reached (Figure 11). Evidently, some factor in addition to interplant competition was influencing the RGR of the snap bean plants.

The total dry weights of 'OSU 1604' and 'OSU 58' were significantly greater than those of the other three cultivars (Table 29). Although the cultivar x sample date interaction was not statistically significant, the advantage of the 'OSU' cultivars appeared to be greatest at sample 1. This suggests the young plants of the 'OSU' cultivars had superior growth rates. Previously discussed results have shown that they have superior NAR (Table 27). In addition, they have greater leaf areas during early development because of their larger leaves (Tables 18 and 21).

As crop development progressed, the RGR declined because of lower NAR and LAR.

### Crop Growth Rates

Crop growth rates (CGR) were calculated using the mean total dry weights from three replications. The data have been statistically analyzed. The range of peak CGR, between 15 and 19 grams per m<sup>2</sup> per day, was in accord with values reported for similar leguminous crops (26, 36).

Among the cultivars, distinct differences were found in CGR (Table 30). During the prebloom period, between samples 1 and 2, 'OSU 1604' and 'OSU 58' had appreciably higher growth rates than either 'Gallatin 50' or 'L-81.' After initial bloom, the CGR of the cultivars depended on the timing and intensity of their reproductive development. 'OSU 1604,' 'OSU 58' and 'L-81,' the cultivars having an early development of reproductive sink potential, reached their peak CGR during the 2-week period immediately after initial bloom. Later, between samples 3 and 4, the CGR of these cultivars declined. 'Gallatin 50' and 'Keystone 4672,' the cultivars having a delayed development of reproductive sink potential, attained their peak CGR between samples 3 and 4. During the early reproductive period, their CGR were only slightly greater than during the prebloom period.

The superior CGR of 'OSU 1604' and 'OSU 58' during the pre-bloom period was a function of both a higher NAR and greater LAI (Table 31). During the early period of reproductive development, the



Table 30. The effect of plant population densities on the crop growth rates (CGR)<sup>z</sup> of five snap bean cultivars during three time periods. Experiment 2, 1972.

Cultivar	Days from Planting	Population density (plants/m <sup>2</sup> )								Cultivar means
		91.42	76.16	63.39	43.90	36.55	30.43	21.10		
OSU 1604	28-42	13.52	12.05	14.43	15.32	15.46	13.79	11.46	13.72	
	42-57	23.88	18.71	16.41	18.32	16.77	16.43	20.48	18.72	
	57-70	7.32	23.98	11.04	7.28	13.79	11.39	3.59	11.20	
OSU 58	28-42	11.09	13.80	12.39	15.40	13.16	11.57	12.21	12.80	
	42-57	14.95	14.39	19.84	12.83	13.18	14.13	13.99	14.76	
	57-70	25.50	16.81	7.56	11.90	10.48	12.75	6.41	13.06	
Gallatin 50	28-42	10.45	12.37	8.69	9.88	11.43	11.26	10.92	10.71	
	42-57	15.16	10.29	14.83	16.25	13.44	11.08	11.56	13.23	
	57-70	24.52	21.75	18.23	13.47	17.35	18.75	14.01	18.30	
L-81	28-42	10.44	11.86	12.04	9.51	9.84	11.18	10.19	10.72	
	42-57	24.94	18.71	19.49	16.21	17.88	12.10	10.15	17.07	
	57-70	6.65	6.11	8.97	19.64	10.95	12.84	14.64	11.40	
Keystone 4672	28-42	13.08	13.57	13.82	9.74	12.17	12.62	9.52	12.07	
	42-57	17.96	9.61	10.12	16.31	13.70	11.76	12.87	13.19	
	57-70	15.06	28.44	14.32	18.31	17.91	12.66	7.01	16.24	
Population means	28-42	11.72	12.73	12.27	11.97	12.41	12.08	10.86		
	42-57	19.38	14.34	16.14	15.99	15.00	13.01	13.81		
	57-70	15.81	19.42	12.02	14.12	14.09	13.68	9.13		

<sup>z</sup> CGR expressed as dry weight gained (grams) per m<sup>2</sup> of soil surface area per day.

Table 31. The relationships between the crop growth rates (CGR), the net assimilation rates (NAR) and the leaf area indices (LAI) of five bush snap bean cultivars during three sample periods. Experiment 2, 1972.

Days from Planting	Cultivar	CGR (g/day)	NAR (mg/dm <sup>2</sup> /day)	LAI
28-42	OSU 1604	13.72	66.97	2.15
	OSU 58	12.80	65.03	2.05
	Gallatin 50	10.71	62.95	1.77
	L-81	10.72	60.81	1.81
	Keystone 4672	12.07	67.54	1.88
		CGR vs NAR: $r = 0.79$		
		CGR vs LAI: $r = 0.97^{**}$		
42-57	OSU 1604	18.72	53.62	3.53
	OSU 58	14.76	45.97	3.22
	Gallatin 50	13.23	36.14	3.67
	L-81	17.07	48.08	3.50
	Keystone 4672	13.19	35.81	3.79
		CGR vs NAR: $r = 0.96^{**}$		
		CGR vs LAI: $r = -0.36$		
57-70	OSU 1604	11.20	50.47	2.38
	OSU 58	13.06	46.63	2.74
	Gallatin 50	18.30	45.35	4.17
	L-81	11.40	34.09	3.43
	Keystone 4672	16.24	39.40	4.04
		CGR vs NAR: $r = 0.01$		
		CGR vs LAI: $r = 0.83$		

\*\*p < .01

superior CGR of the 'OSU' cultivars and 'L-81' were clearly a function of their higher NAR; in fact, the cultivars with the greatest LAI, 'Gallatin 50' and 'Keystone 4672' had the lowest CGR. For the final sample period, the relative effects of NAR and LAI on the CGR of the cultivars is difficult to ascertain because of the senescence of leaves. The cultivars having a higher LAI tended to have a higher CGR; nonetheless, the fact that the CGR of 'Gallatin 50' and 'Keystone 4672' increased over that of the previous period, despite a net reduction in their LAI, suggests an increase in NAR was mainly responsible for the rise in their CGR.

Plant population density did not influence CGR during the pre-bloom period (Table 30). During the period of reproductive development, the CGR generally increased as population density increased. The variability of the CGR data precluded a meaningful comparison of the cultivar responses to density.

In Figure 13, the mean CGR at each population density has been plotted against the corresponding LAI. The overall relationship for the three sample periods fits neither the optimum nor the critical LAI concept.

During the prebloom period, CGR was not significantly affected by LAI. The range of LAI was between 1.25 and 2.50; all considerably below the critical LAI of 4 that has been reported for Phaseolus vulgaris L. (62) and soybeans (26, 96). The lack of correlation

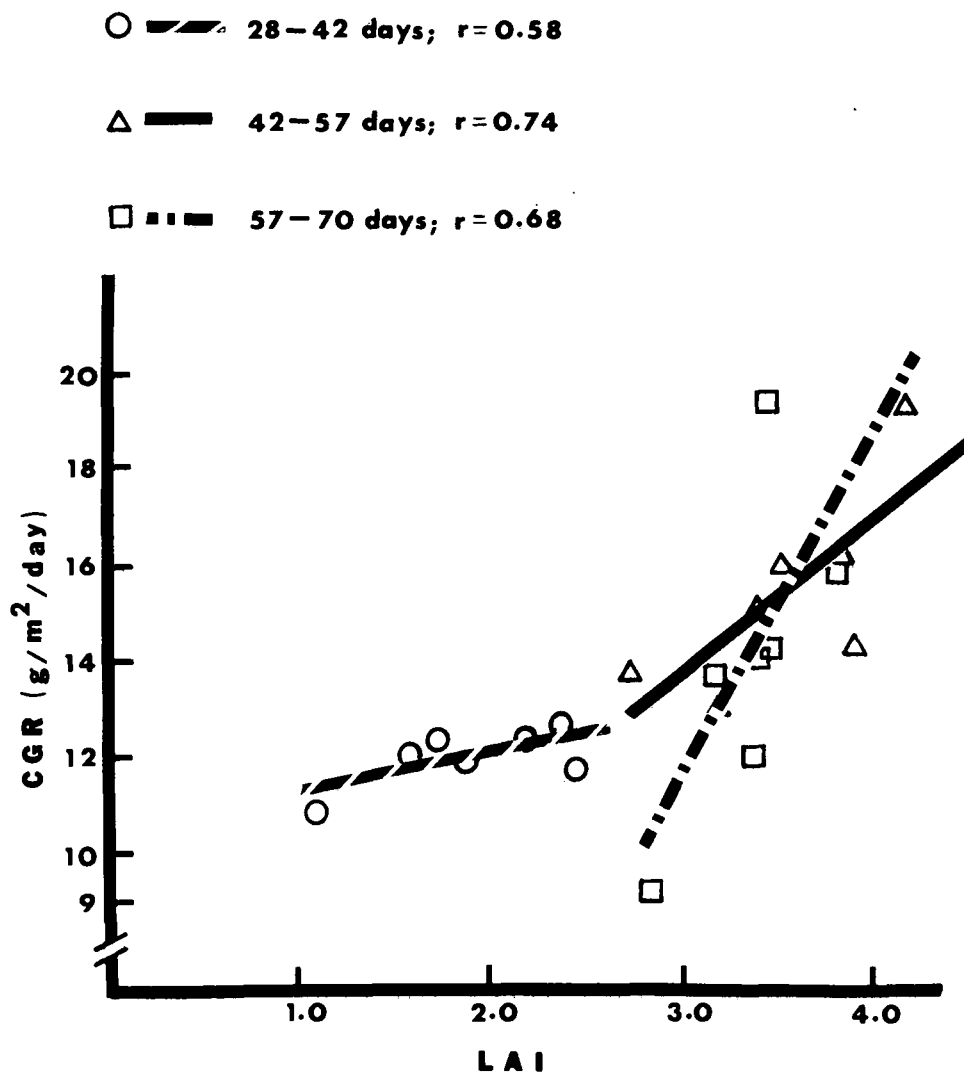


Figure 13. Relationship between the leaf area index and crop growth rates of bush snap beans during three sample periods (days from planting). Experiment 2, 1972.

between LAI and CGR was a result of the precipitous decline in NAR as LAI increased (Table 10).

CGR and LAI were not significantly correlated during either one of the two reproductive sample periods; however, the lack of correlation mostly resulted from the variability of the data. When the data from the two periods were combined, a highly significant, linear correlation was found. The correlation was partly a function of the constancy of NAR as LAI increased. Contrary to the results from the prebloom period, the CGR continued to increase as LAI exceeded 4, during the reproductive period. The constancy of CGR during the prebloom period, therefore, was not the result of a uniform effective foliar canopy across the entire range of population densities.

The results suggest the CGR was appreciably influenced by the developmental activities of the plants, especially reproductive development. These activities influenced the assimilatory efficiencies of the leaves, as previously discussed. Eastin and Gritton (36), working with peas (Pisum sativum L.), found the CGR increased at higher densities during reproductive development despite a net decline in LAI. They attributed the response to the positive effect of sink potential on photosynthetic apparatus.

### Dry Matter Distribution

Harvest indices (HI) have been calculated for the final samples of both experiments (Table 32). In both experiments, the higher yielding cultivars had a higher HI. This result is contrary to the findings of Wallace and Munger (107) that showed a poor correlation between the seed yields and HI of dry bean cultivars. The effect of population density on HI was inconsistent. In Experiment 1, population density did not have a statistically significant effect on HI; although, increasing density tended to decrease HI. In Experiment 2, the HI increased significantly as population density increased. Previous studies have shown HI either remained constant or declined slightly as density increased (62, 81, 89).

The calculation of dry matter ratios, such as HI, is not a satisfactory method of expressing dry matter distribution, because they do not show how they were affected. A better method of expressing dry matter distribution has been discussed by Brouwer (18). In accordance with this method, the dry weights of various plant components were plotted against the total above ground dry weight per plant for the four sample dates of Experiment 2 (Figures 14 and 15). The plant components included: the functional leaves, the pods, and the structural and miscellaneous organs. Leaves too small or too senescent to be considered functional assimilators were included in the structural and miscellaneous component.

Table 32. The effect of plant population densities and cultivars on the harvest index (HI)<sup>z</sup> of bush snap beans. Experiments 1 and 2, 1972.

Population density (plants/m <sup>2</sup> )	Experiment 1	Experiment 2
109.84	--	0.465
91.42	0.519	0.476
76.16	0.497	0.475
63.39	0.513	0.463
52.73	--	0.442
43.90	0.508	0.452
36.55	0.535	0.450
30.43	0.527	0.434
25.35	--	0.432
21.10	0.521	0.413
LSD, 5%	ns	0.025
1%	ns	0.034
<u>Cultivar</u>		
OSU 1604	0.635	0.568
OSU 58	0.642	0.531
Gallatin 50	0.461	0.360
L-1	0.328	--
L-81	--	0.431
Keystone 4672	0.521	0.361
LSD, 5%	0.023	0.046
1%	0.034	0.067

<sup>z</sup> Harvest index calculated as dry weight pods/total plant dry weight.

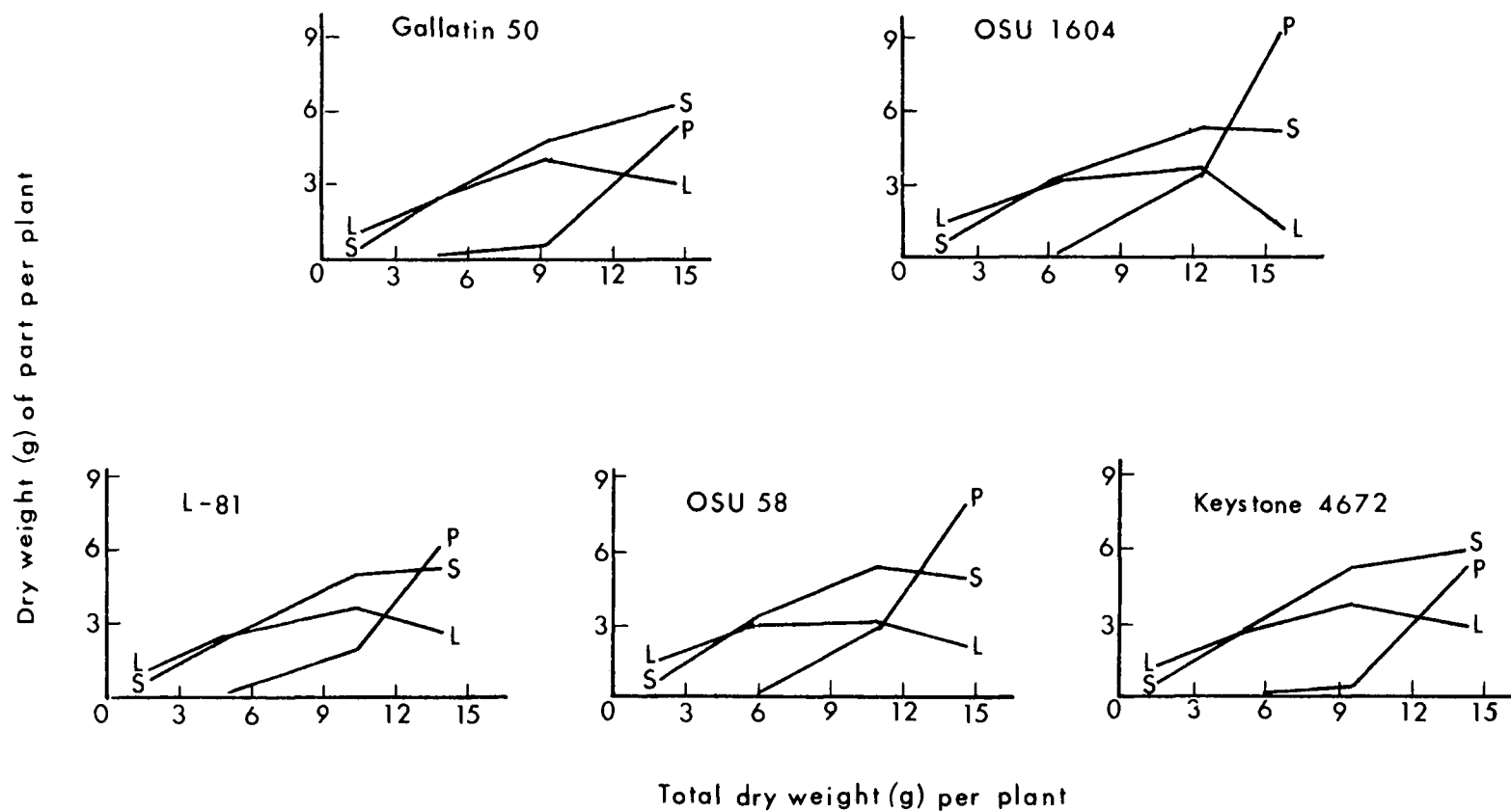


Figure 14. The seasonal distribution of dry matter among leaves (L), pods (P) and structural organs (S) by individual plants of five cultivars of bush snap beans. Experiment 2, 1972.



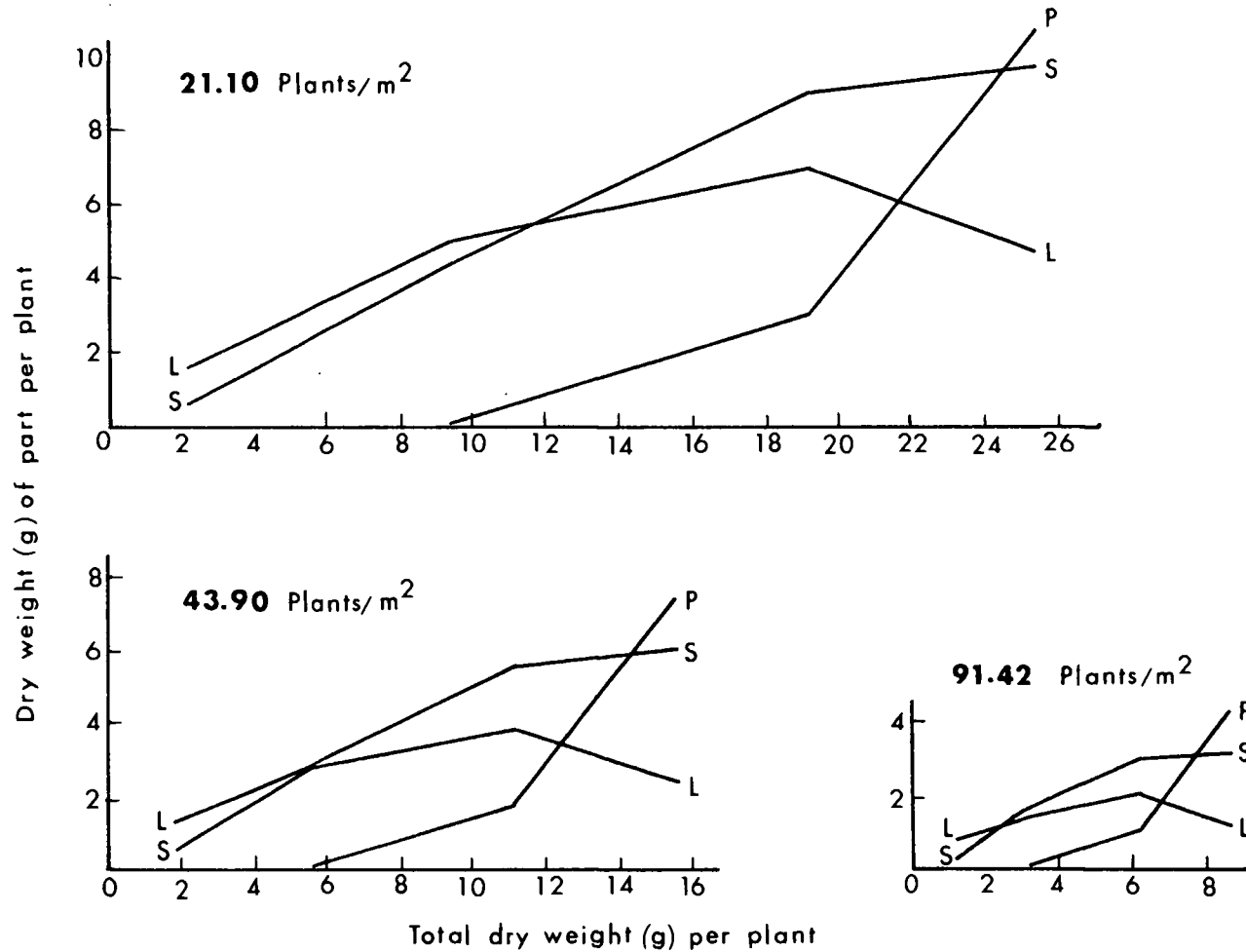


Figure 15. The seasonal distribution of dry matter among the leaves (L), pods (P) and structural organs (S) by individual plants of bush snap beans at three population densities. Experiment 2, 1972.

Among the cultivars, no obvious differences were found in dry matter distribution during the prebloom period (Figure 14). Leaf dry weight was the major component of the total dry weight at sample 1, which suggest that leaf growth was favored during early development. The proportionally greater distribution of dry matter to the structural component between samples 1 and 2 corresponded to the period of initial branch development.

After the onset of reproductive development, the patterns of dry matter distribution varied considerably among the cultivars. During early reproductive development, the proportional distribution of dry matter to the pods was much greater for 'OSU 1604,' 'OSU 58' and 'L-81' than it was for 'Gallatin 50' and 'Keystone 4672.' During the later part of reproductive development, the proportion of dry matter distributed to the pods increased for all cultivars. These results suggest the higher HI of the 'OSU' cultivars was mainly a result of the greater initial growth rate of their reproductive component. In addition, the relative lengths of the vegetative and reproductive developmental phases may have had a slight influence on the HI of the cultivars. Previously discussed results have shown 'Gallatin 50' and 'Keystone 4672' bloomed two and four days later than the other cultivars.

The pattern of dry matter distribution was not appreciably affected by plant population density (Figure 15). The change in dry

weight of a plant component per unit change in total plant dry weight was the same at all densities; a fact manifested in the constancy of the slopes of any given component over any developmental phase. The greater HI at the higher population densities was a function of the growth rates of the plants during the periods of reproductive development.

## SUMMARY AND CONCLUSIONS

The pod yield per area of snap beans responded parabolically to population density; increasing as population density approached an optimum level and then declining gradually when the density exceeded that level.

The component analysis of snap bean yield was difficult because of compensatory relationships between the components, the cyclic pattern of pod set and the marketable product being an immature reproductive organ. Nevertheless, the results showed that as population density increased the number of pod bearing racemes per area increased toward an asymptote and the number of pods per raceme and the average pod weight declined linearly. The optimum density was that density at which the number of racemes per area was increasing at a rate only sufficient to compensate for reductions in pods per raceme and average pod weight.

The first component to complete development was the number of pod bearing racemes. Because of the limitations imposed by a single destructive harvest, racemes forming after a certain time would not be able to produce a significant yield of marketable pods. The number of pod bearing racemes per plant was the component most sensitive to interplant competition. As population density increased, it declined much more rapidly than either the number of pods per raceme

or the average pod size. A substantial reduction in the number of pods per raceme occurred late in the development of the crop. This was associated with the abscission of many pods that appeared to be parthenocarpic. The reductions in pod number per raceme and pod size were probably a function of increased levels of intraplant competition at higher densities.

A substantive analysis of plant growth and development was made in Experiment 2. Unfortunately, the predicted optimum population densities were beyond the range of densities investigated in this experiment; therefore, the explanations offered for the parabolic yield-population density relationship are tenuous.

As population density increased, the number of branches per area increased to a peak level and then declined. The rate of decline of branches per plant exceeded that of pod bearing racemes per plant. Therefore, an increasing percentage of the racemes were borne directly on the main stem, probably in the axils of older leaves. This would increase intraplant competition between racemes and could be responsible for the reduced number of pods per raceme and smaller pod size found at higher densities.

The effect of population density on leaf area ratio (LAR) varied with the stage of crop development. During the prebloom period, LAR increased slightly as density increased. This was partly a manifestation of the reduced branching at the higher densities. At the final

sample, LAR decreased slightly as density increased, probably because of the greater senescence of leaves at the higher densities.

The LAR decreased for all population densities as crop development progressed. This was partly responsible for a concomitant decline in the relative growth rate (RGR) of the plants.

The specific leaf area (SLA) increased to a constant level as population density increased. As crop development progressed, an increasing range of the higher densities had a constant SLA. The results suggest the increases in SLA were related to increased levels of mutual shading. The changes in LAR and SLA associated with increasing population density do not appear to be significant affectors of the pod yield-population density relationship.

The plants at all densities gained leaf area until the final stage of crop development, when a net loss of leaf area occurred because of senescence. During early development, the gain in leaf area was proportionally greater at the lower densities. At the final stage of crop development the loss of leaf area was proportionally greater at the higher densities, possibly because an older average leaf age. This would increase intraplant competition and could be partly responsible for the reductions in the number of pods per raceme and the average pod size at the higher densities. The lower leaf area per raceme at the higher densities could also be affecting these reductions.

Leaf area index (LAI) increased toward an asymptote as population density increased. The increasing LAI was associated with increasing pod yields; however, the complexity of the relationship between crop growth rate (CGR) and LAI suggests the pod yield-population density response was not entirely a simple function of the effect of LAI on the net production of dry matter.

The relationship between LAI and CGR depended on the stage of crop development. During the prebloom period, the CGR was constant at approximately  $12.5 \text{ g per m}^2$  per day across a range of LAI from 1.25 to 2.5. The constancy of CGR resulted from a precipitous linear decline in NAR as LAI increased. During the period of reproductive development, the CGR increased linearly as LAI increased and attained a value of  $18 \text{ g per m}^2$  per day at the highest LAI recorded, 4.25. The linear association between LAI and CGR during the reproductive period was a function of the constancy of NAR across a range of LAI from 2.8 to 4.25.

The overall relationship between LAI and CGR fits neither the optimum nor the critical LAI concept. An explanation of the unusual crop growth rate pattern can be based on the interaction between sink potential and the efficiency of the leaves. During the prebloom period, the major sink would be the developing branches. More branches were developing per unit leaf area at the lower densities, probably because of greater penetration of light through the foliar canopies.

If branch development stimulates leaf efficiency, the NAR of the leaves at the lower densities would be increased relative to those at the higher densities. This effect, in conjunction with increased mutual shading, could result in the steep linear decline in NAR as LAI increased. During reproductive development, the sink demand, measured as the leaf area per raceme, was stronger at the higher densities. This would increase the efficiency of the leaves at the higher densities relative to those at the lower densities; as a result, the NAR could remain relatively constant as LAI increased, despite greater degrees of mutual shading.

This analysis of the CGR patterns suggests that poor light distribution limits yield more by inhibiting the initiation and development of a superstructure for reproductive development, than by limiting crop growth during the pod filling stage. The constancy of the CGR during the prebloom period does not support the hypothesis that increased yields at higher population densities are a result of a reduction in the length of time required for the attainment of a critical LAI. An alternative explanation is that increasing population density increases the amount of reproductive sink developing during the initial period of reproductive development.

Based on field observations and a limited amount of data, population density did not influence either the date of initial bloom or the timing of other phases of plant development. In addition, the



number of nodes on the main stem prior to the formation of the terminal inflorescence was not affected by population density.

The proportional distribution of dry matter among the leaves, pods and structural organs was not influenced by population density. Harvest index (HI) declined as density decreased in Experiment 2; however, the lower HI was a function of the growth rate rather than the pattern of distribution. In Experiment 1, HI was not affected by density.

The modified reciprocal model

$$w^{-\theta} = \alpha + \beta \rho$$

was used to compare the pod yield-population density responses of the cultivars. A common  $\theta$  value of 0.854 in Experiment 1 and 0.836 in Experiment 2 gave statistically acceptable fits for the data of all cultivars. A  $\theta$  of 0.85 may be an acceptable standard value for future snap bean research. Experience with fitting the model showed, however, that a wide range of common  $\theta$  values gave acceptable fits.

The variation in the  $\alpha$  and  $\beta$  constants of the cultivars did not conform to the theory that  $\alpha$  is a measure of genetic potential and  $\beta$  is a measure of environmental potential. In Experiment 1, a common  $\alpha$  was found for the five cultivars, but the  $\beta$  varied significantly. In Experiment 2, both the  $\alpha$  and  $\beta$  values of the cultivars varied significantly.

The modified reciprocal model was a valuable tool for revealing essential differences in the pod yield-population density responses of snap bean cultivars; however, the  $\theta$  parameter was difficult to fit accurately and the variation of the  $\alpha$ ,  $\beta$  and  $\theta$  parameters was difficult to interpret biologically. If future research is not able to determine that the parameters have biological significance, a more empirical but more easily fitted model, such as a reciprocal polynomial, should be used in snap bean research.

The model revealed that the optimum population densities of the cultivars differed appreciably. This suggests that as new snap bean cultivars are released they should be tested to determine their particular optimum planting densities. In Experiment 1, the 'OSU' cultivars had the highest optimum densities, but in Experiment 2 the cultivars with small leaves, 'L-81' and 'Keystone 4672,' had the highest.

The ranking of the cultivars generally was not affected by densities between 21- and 110 plants per m<sup>2</sup>. In both experiments and at all densities, the 'OSU' lines gave superior pod yields. This result suggests that population density will not be a significant confounding factor in the development or selection of high yielding snap bean cultivars.

The cultivars differed significantly in the component configurations of their pod yields, however, no statistically significant cultivar

x population density interactions were found among the components. The smaller leaved cultivars had greater numbers of pod bearing racemes. They also had, however, fewer pods per raceme and smaller pods, which suggests a greater intensity of intraplant competition. Assuming the use of a single destructive harvest, the number of racemes with marketable pods that could develop on the small leaved cultivars, to compensate for their smaller pods and fewer pods per raceme, would be limited by time.

In both experiments and at all densities, the component characteristic most closely associated with high pod yield was large average pod size. The superior cultivars, 'OSU 58' and 'OSU 1604,' had average numbers of racemes per plant and pods per raceme, but had distinctly larger than average pods. This suggests that breeders should select for cultivars with large pods. Considering the snap bean grade standards that discriminate against beans of large sieve size, however, the pod size would have to be increased by means of longer pods rather than thicker ones. The potential for doing this may be limited. Future work should be directed toward increasing the number of racemes per plant without reducing the number of pods per raceme or the pod size. The genetic and physiological bases for the apparent association of small leaves and small pods should be investigated.

The growth and developmental characteristics of the cultivars were compared in Experiment 2. The cultivar x population density interactions were not significant for most of the parameters examined. The general lack of interaction can be attributed to the fact that the cultivars differed mainly in temporal development and dry matter distribution; the population density did not appreciably influence either of these processes. Any subtle differences in cultivar response to population density were probably being masked by the large cultivar x sample date interactions.

The highest yielding cultivars, 'OSU 1604' and 'OSU 58,' were characterized by a rapid initial development of reproductive sink and a concomitant halt to most vegetative growth. This was manifested as a high harvest index. They added few racemes or pods after the initial flush of reproductive development. Their large average pod size is partly a function of the concentrated and early reproductive development. 'L-81' also had a rapid initial development of reproductive sink, but it continued, afterwards, to grow vegetatively and set more pods. The two low yielding cultivars, 'Gallatin 50' and 'Keystone 4672,' were characterized by a poor initial development of reproductive sink and continued vegetative growth and development during the early reproductive period. Most of their reproductive sink developed approximately two weeks after the first bloom. They had low harvest indices.

The poor initial reproductive development of 'Gallatin 50' and 'Keystone 4672' did not result from intraplant competition between vegetative and reproductive growth. Their NAR values were lowest during the 2-week period after the initial bloom. Later, when their reproductive development increased, their NAR also increased. These results suggest an inadequate sink during early reproductive development rather than a high level of intraplant competition.

The results indicate that a concentrated development of reproductive sink is an important selection criterion regardless of the population density.

Among the cultivars, a high leaf area during the period of reproductive growth was not associated with either a high CGR or a high pod yield. In fact, the cultivars having the highest leaf areas during this period tended to have the lowest pod yields, because the leaves had grown instead of the reproductive organs.

Evidently the leaf area developing after bloom makes only a limited contribution to the growth of the marketable pods. Based on the concept of the nutritional unit, most of the leaf area developing after bloom would be associated with the development of new racemes. and would probably not be a significant source of assimilate for the pods on the racemes that had developed earlier. Because of the temporal limitations imposed by a single destructive harvest, these new racemes would not have time to develop marketable pods. In this

study, all of the cultivars had approximately the same leaf area at initial bloom.

During the early weeks of plant development, prior to significant branch development, the leaf area of a plant was mainly a function of the leaf size. Therefore, smaller-leaved cultivars would necessarily have a smaller leaf area during this period. For this reason, they would have a slower rate of early growth. In addition, they would offer less shade competition to weeds and could be more susceptible to insect damage.

The architectures of the foliar canopies of the cultivars did not differ significantly in assimilatory efficiency. The NAR of the five cultivars declined at the same rate per unit increase in LAI during the prebloom period, and remained constant regardless of LAI during the reproductive periods. The LAI levels reached by the crops were generally under 4; probably not high enough to disclose any advantages that small leaves might offer.

In Experiment 2, however, the small leaved cultivars had a slower rate of decline in branches per plant with increasing population density. This cultivar  $\times$  population density interaction was most likely a manifestation of differences in the canopy architectures of the cultivars. Branch development, therefore, seems to be more sensitive than NAR to the nature of light distribution in the crop canopy.

This interpretation supports the previously discussed idea that poor light distribution limits yield more by inhibiting the development of the superstructure for reproductive development than by limiting crop growth potential.

Significant differences were found in the assimilatory efficiencies of the leaves of the cultivars. The two high yielding cultivars, 'OSU 1604' and 'OSU 58' had the highest NAR at any measured LAI, during the prebloom period. The efficiency of the individual leaf could have an important effect on snap bean yield because of the nature of the nutritional unit and the temporal limitations on yield. Further research should be undertaken to determine the extent of and the physiological basis for differences in the NAR of snap bean cultivars.

A significant negative correlation was found between the specific leaf area (SLA) of a cultivar during the prebloom period and its NAR. Considering the ease of measuring SLA, it may be a useful criterion for indirect selection of improved leaf efficiency. More research should be undertaken to establish a physiological basis for the relationship between these two parameters.

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Appendix Table 1. Daily maximum and minimum temperatures recorded at official weather station at Oregon State University, Corvallis, Oregon, 1972.

Day of Month	Month							
	May		June		July		August	
	Max	Min	Max	Min	Max	Min	Max	Min
1	59	35	71	53	84	54	77	48
2	67	37	75	45	85	55	79	47
3	70	42	79	50	92	58	77	51
4	73	43	68	46	94	51	93	52
5	75	40	79	44	94	52	95	55
6	69	39	82	56	84	49	97	59
7	64	46	79	53	75	48	103	56
8	57	37	75	56	74	53	105	56
9	60	39	75	53	67	45	98	56
10	65	36	61	52	72	47	93	46
11	70	40	63	49	73	48	86	46
12	76	46	66	44	82	53	81	51
13	82	51	72	49	85	60	72	40
14	84	47	78	54	85	56	76	50
15	79	49	73	55	85	58	76	53
16	61	53	64	43	91	63	74	49
17	59	41	68	45	97	59	68	53
18	54	44	76	48	98	53	72	51
19	61	48	78	52	76	51	73	51
20	75	51	81	46	85	55	81	52
21	63	50	77	53	87	50	80	57
22	60	50	68	47	85	47	79	53
23	62	43	72	51	90	47	79	55
24	57	41	65	47	85	48	84	50
25	59	42	62	52	80	46	84	52
26	69	45	65	47	80	46	89	59
27	81	48	71	54	82	45	95	60
28	85	52	81	52	85	53	98	60
29	88	47	87	53	92	54	95	52
30	77	41	83	51	91	55	91	54
31	77	42	-	-	95	52	81	56